A MULTI-SCALE EXAMINATION OF STOPOVER HABITAT USE BY MIGRANT SHOREBIRDS

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CHAPTER I

SPATIOTEMPORAL SCALING OF NORTH AMERICAN CONTINENTAL INTERIOR WETLANDS: IMPLICATIONS FOR SHOPREBIRD CONSERVATION

ABSTRACT

Within interior North America, erratic weather patterns and heterogeneous wetland complexes cause wide spatio-temporal variation in the resources available to migrating shorebirds. Identifying the pattern-generating components of landscape-level resources and the scales at which shorebirds respond to these patterns will better facilitate conservation efforts for these species. We constructed descriptive models that identified weather variables associated with creating the spatio-temporal patterns of shorebird habitat in ten landscapes in north-central Oklahoma. We developed a metric capable of measuring the dynamic composition and configuration of shorebird habitat in the region and used field data to empirically estimate the spatial scale at which shorebirds respond to the amount and configuration of habitat. Precipitation, temperature, solar radiation and wind speed best explained the incidence of wetland habitat, but relationships varied with time and among wetland types. Shorebird occurrence patterns were best explained by habitat density estimates at a 2km scale. This model correctly classified 85% of shorebird observations. At this scale, when habitat density was low, shorebirds occurred in 6% of surveyed habitat patches but occurrence reached 56% when habitat density was high. Our results suggest scale dependence in the habitat-use patterns of migratory shorebirds.

We discuss the advantages of this approach and how integrating this information into conservation efforts may improve conservation strategies and management practices.

Key words: Kernel density estimation, landscape metric, migration, multi-scale, shorebird habitat, weather patterns, wetland complex.

INTRODUCTION

Environmental variation concurrently influences the response of biological communities at multiple spatial scales, and a primary objective of landscape ecology is to determine the role scale plays in influencing ecological patterns and processes (Turner et al. 1989; Turner 2005). Broad and fine scale dynamics determine the composition of species within a biological community (Ricklefs 1987; Cushman and McGarigal 2004a) and observed patterns in the abundance of organisms depends on the spatial and temporal scale of observations (Allen and Star 1982; Carlile et al. 1989; Turner et al. 2001). Moreover, organisms function within a range of scales, especially within and among different life history stages such as breeding, dispersal and migration (Addicott et al. 1987; Wiens 1989; Lindenmayer 2000; Moore 2000). To understand species-habitat relationships, researchers must consider the scale of environmental patterns and understand how species are affected by these patterns at different scales (Wiens 1989; Levin 1992; Turner 2005). However, we often limit our understanding of these species-habitat relationships by only examining them at one or a few arbitrarily chosen scales that are often not among the range of scales unique to the phenomenon of interest (Wheatley and Johnson 2009). Failure to account for scale-dependent influences may confound and confuse interpretation of results and may make generalizations about organisms inappropriate (Wiens 1989; Cushman and McGarigal 2004b). Thus, an understanding of the role of scale in species-habitat relationships is needed before we develop species-habitat models.

The relationship between migratory birds and habitat exists within a hierarchal system of interconnections (Moore 2000). Within this hierarchy, broad scale patterns such as weather and land cover constrain finer scale patterns in habitat composition and configuration within a region. At even finer scales, habitat-use patterns are further constrained by factors such as habitat quality and biological interactions within a single habitat patch. Abiotic and biotic interactions among levels in the hierarchy generate the patterns that structure the spatial distribution of migratory birds. One way to understand the relationship between migratory birds and habitat factors among scales is to decompose the system into levels and examine species-habitat patterns within each level of the hierarchy (Urban et al. 1987). Because species respond to the environment among a unique range of scales (Levin 1992) and no single scale is correct for describing species-habitat relationships (Wiens 1989), multi-scale approaches are often used to describe species-habitat relationships among birds (Thompson and McGarigal 2002; Graf et al. 2005; Boscolo and Metzger 2009). Identifying the pattern-generating components and the scales at which migratory birds respond to these patterns will better facilitate conservation efforts for these species. In particular, knowledge of the scale dependence of migratory species will lead to more accurate and efficient census and research techniques and improved refuge design and management practices.

A multi-scale approach is necessary to understand, manage, and predict the behavior of migratory birds that encounter complex landscapes that are continually changing (Hay et al. 2001). Shorebirds encounter a spatially and temporally shifting mosaic of habitat conditions during their annual southward and northward migrations. (Davis and Smith 1998a; Skagen et al. 1999; Skagen et al. 2008a). This is particularly evident during migration through central North America, where shorebirds use a variety of wetlands as stopover sites to replenish depleted energy and nutrient reserves that are critical for the birds to continue and complete their migration (Skagen and Knopf 1993; Skagen et al. 2005). Within the continental interior, shorebirds encounter clusters of heterogeneous wetland complexes (Weller 1988) composed of wetlands

with different inundation periods (e.g., seasonal, temporary, and permanent hydroperiods) and different wetland types (e.g., lacustrine, riverine, palustrine and anthropogenic-created systems). Furthermore, within a landscape, wetland complexes, which act as functional units because they are connected by common precipitation, surface and groundwater inputs, are critical to migrant shorebirds (Naugle et al. 2001; Johnson et al. 2010).

Many shorebird species are associated with wetland habitats during migration and primarily rely on saturated soils and shallow water within and around wetlands to acquire food resources. The types of wetlands used by shorebirds in the continental interior range from ephemeral wet prairie and agricultural sheetwater, to managed wastewater impoundments and livestock ponds, to more permanent lakes and rivers. In the interior of North America, capricious weather patterns produce an unstable wetland landscape with transient and unpredictable resources. Consequently, habitats available for migratory shorebirds can vary widely depending on seasonal and annual weather patterns (Skagen et al. 2008a). For example, severe and erratic weather patterns in the Southern Great Plains can produce highly dynamic wetland complexes. The region is subject to extreme dry and wet periods (Woodhouse and Overpeck 1998), and seasonal weather systems consist of fast moving and severe storm cells that can rapidly inundate relatively small and discrete areas (Ashley et al. 2003; Oklahoma Climatological Survey (OCS) 2010). During dry periods, permanent and semi-permanent wetlands provide abundant shorebird habitat as mud becomes exposed in lakes, rivers, and ponds, but shallow temporary wetlands such as ephemeral pools and agricultural sheetwater become rare as dry conditions persist. However, these temporary wetlands can provide habitat after heavy precipitation and during wet periods when the exposed mud of more permanent wetlands becomes inundated by water. As illustrated by the dynamic nature of wetland complexes, the availability of habitat and food supplies can be quite unpredictable for migratory shorebirds. As a result, the occurrence and movement patterns

of migratory shorebirds through interior North America can vary greatly within and among seasonal and annual migration periods (Colwell 2010).

Wetlands used by migratory shorebirds within central North America have been severely impacted by the rapidly changing landscape. For example, it is estimated that 50-85% of the wetlands in the Southern Great Plains have been destroyed since the 1780s (Dahl and Allord 1996) and most of the remaining wetlands have little legal protection (Haukos and Smith 2003; van der Valk and Pederson 2003). Moreover, because these wetlands are embedded within agricultural landscapes, many of them are degraded by agricultural practices that increase sedimentation and nutrient and contaminant accumulation (Lou et al. 1997; Detenbeck et al 2002; Skagen et al 2008b), change vegetation structure and composition (Smith and Haukos 2002) and negatively impact invertebrate prey resources (Davis and Bidwell 2008). Alteration of hydrological regimes for crop and livestock production and waterfowl management also impacts the suitability of wetlands for foraging shorebirds (Taft et al. 2002; Koper and Schmiegelow 2006). More recently, predictions of climate change and more intensive agriculture suggest continued alteration and loss of prairie wetlands in the future (Poiani and Johnson 1991; Tilman 2001; Johnson et al. 2010). Recent research has suggested that population limitation of shorebirds in part occurs during migration (Baker et al. 2004; Morrison 2006), and intrinsic factors related to an interior migration strategy increases the vulnerability of transcontinental migrants to population decline when compared to coastal and oceanic migrants (Thomas et al. 2006). With nearly half of North American shorebird species believed to be declining (Brown et al. 2001; Morrison et al. 2001), these large-scale habitat changes have raised serious concerns about maintaining an adequate network of stopover sites for migrant shorebirds (Skagen 2006).

Conservation efforts for transcontinental shorebird migrants need to develop approaches that identify landscapes that provide critical wetland habitat and incorporate the shifting distributions of habitats and birds on the landscape (Skagen et al. 2005; Colwell 2010).

Understanding the dynamic relationship between weather patterns and wetland habitat is essential to these efforts. Predictions of climate change make understanding the effect of current weather patterns on the spatial distribution and availability of wetland habitats even more imperative. However, our current understanding of the relationship between environmental patterns and how migratory shorebirds respond to these patterns across different spatial and temporal scales is inadequate for the development of conservation strategies (Skagen et al. 2005). Heterogeneous wetland complexes and the broad dispersion and erratic occurrence of migratory shorebirds throughout the Southern Great Plains makes a quantitative evaluation of shorebird-habitat relationships at appropriate spatio-temporal scales challenging. Alternatively, the effectiveness of site-based approaches is limited because shorebirds typically exhibit low site fidelity and greater opportunism as a consequence of the unpredictable nature of suitable habitat (Skagen et al. 2008; Colwell 2010). In addition, the occurrence and abundance of birds at a site is likely related to both the scale range at which birds perceive the environment and/or by aspects of the surrounding environment occurring at different scales (van Rumbsberg et al. 2002; Ewers and Didham 2006; Boscolo and Metzger 2009). To meet these challenges, an effective approach must consider the relationship between weather patterns and the distribution of wetland habitats among broad landscapes over time, and the response of shorebirds to these patterns among a range of scales. However, we are unaware of any studies that have integrated scaling principles into an experimental design used to describe how these relationships affect the distribution of migratory shorebirds.

This study examined the relationship between shorebird habitat density and shorebird distribution among ten broad scale landscapes in north-central Oklahoma. Our objectives were to: (1) Construct descriptive models that identified weather variables associated with creating the spatio-temporal patterns of shorebird habitat, (2) develop a metric capable of measuring the dynamic composition and configuration of shorebird habitat in the region, and (3) use field data

to empirically estimate the spatial scale at which shorebirds respond to the amount and configuration of habitat. Specifically, we developed a geographic information system (GIS) that identified areas of potential shorebird habitat within each landscape. We performed successive surveys of these areas for the presence of shorebirds and habitat within different wetland types. We used habitat data to calculate estimates of the density of shorebird habitat within landscapes over time. The relationship between shorebird occurrence data and habitat density estimates were modeled to assess the validity of the habitat density estimates and to identify the spatial scale(s) at which shorebirds had the strongest relationship with habitat density.

METHODS

Study area and organisms

We studied shorebird migration in north-central Oklahoma, US. The study area encompassed ten counties that occupied a total area of 24,372 km^2 (Fig. 1.1). Historically, this landscape was comprised of mixed-grass prairie, but now the landscape is dominated by rangeland and cropland (Oklahoma Department of Wildlife Conservation 2006). The region contains a variety of palustrine, lacustrine, and riverine wetlands (Henley and Harrison 2000).

Although many different shorebird species of the order Charadiformes may be encountered during migration through north-central Oklahoma, our research focused on members of two suborders, *Scolopaci* and *Charadrii*. These suborders contain a wide range of species with different habitat associations, however, this research was restricted to those species that migrate through the study area and that rely on wetlands as stopover sites during migration. The spring shorebird migration period within the study area typically begins during late February and ends in early June, while the fall migration period begins in mid-July and ends in October.

Geographic information system

We used Environmental Systems Research Institute's (ESRI) ArcGIS 9.0 (1999-2004) GIS software to assemble base data layers for each county that included countywide 1:25,000 USGS topographical image mosaics and countywide mosaics of 1.0 m resolution 1:12,000 digital ortho-image quarter quadrangles (DOQQs). We assembled DOQQs for six years (2000, 2003-2006, and 2008) as base data (Fig. 1.2). Generally below average precipitation and less shorebird habitat characterized the 2004, 2005 and 2006 images, while above average precipitation and abundant shorebird habitat characterized 2000, 2003, and 2008 images (Oklahoma Climatological Survey 2010).

Within the study area, we randomly placed ten 10-km radius circles (314.16 km^2) that we designated as broad-scale experimental units to represent the total area a migrant shorebird may traverse to locate foraging habitat during a stopover event (Fig. 1.2). The size of broad-scale experimental units was based on radio telemetry research conducted on migrant shorebirds in the Midwestern US that found 90% of radio-tagged birds (n = 110) never traveled >10 km from their release site during a stopover event (Farmer and Parent 1997). We estimated a sample size of ten broad-scale units would be required to detect an effect in shorebird abundance using an *a priori* regression power analysis for sample size (α = 0.05, 1- β = 0.90; Lenth 2006) with variance and effect size estimates from pilot study data.

Within each broad-scale unit, we visually located each potential habitat patch and delineated them as fine-scale experimental units using the GIS (Fig. 1.2). We defined shorebird habitat as areas that potentially contain saturated substrate and shallow water (<16 cm) within wetlands and around wetland edges. Because this study was restricted to those species that rely on wetlands as stopover sites, non-habitat was any area surrounding potential habitat that did not meet these criteria, i.e., dry upland areas. We defined a fine-scale experimental unit as a discrete area of contiguous potential shorebird habitat that was encompassed by a matrix of non-habitat among the DOQQs and during the study period. To delineate fine-scale units, we systematically

examined the entire extent of all base layer DOQQs at a1:10,000 scale within each broad-scale unit. When an area of interest was located, we decreased the map scale over the area for accurate identification and comparison among years. When a discrete patch of shorebird habitat was identified, it was categorized into one of three inundation classes (i.e., temporary, semi-permanent, or permanent) and delineated as a polygon. Temporary, semi-permanent, and permanent inundation classes were defined as habitat present only during wet years, not present in at least one dry year, and present in all years from 2000 to 2009, respectively. Wet and dry years were determined using county climatic data summaries of precipitation data measured from 1971-2000 (Oklahoma Climatological Survey 2010) and visual assessments of all DOQQs.

The fine-scale experimental unit boundaries delineated for temporary and semi-permanent inundation classes encompassed the greatest contiguous spatial extent of potential shorebird habitat among the annual series of DOQQs (Fig. 1.2). The spatial extent between the lowest shoreline edge and the highest shoreline edge of a wetland area among the DOQQs formed the boundaries of fine-scale units in the permanent class (Fig. 1.2). Because of logistical constraints, we did not delineate discrete potential habitat patches < 1,000 m^2 or areas within channeled waterways < 30 m wide. We further improved the accuracy of our data layers by verifying and refining our classifications on 1:2,000 scale color ortho images that we used during field surveys.

Field methods

During each migration period (spring 2007, 2008, 2009 and fall 2007, 2008), we conducted four shorebird surveys on a sample of randomly selected fine-scale units within each broad-scale unit. Each migration period was divided into four 23-day intervals. We estimated a sample size of 13% of the total potential shorebird habitat area in each broad-scale unit would be required to detect an effect in shorebird occurrence using an *a priori* regression power analysis (Lenth 2006) for sample size ($\alpha = 0.05$, $1\text{-}\beta = 0.95$) with variance and effect size estimates from

pilot study data. We therefore surveyed 13-15% of the total area of fine-scale units in each broad-scale unit during each 23-day interval. Within each broad-scale unit, the proportion of fine-scale unit area sampled in each inundation class was equal to the proportion of the total habitat area that each inundation class encompassed.

A software program specifically developed for this project was used to efficiently select and survey fine-scale units that met our sampling requirements. During each survey interval, the program randomly selected the required sample of fine-scale units and an alternate sample within each broad-scale unit. Each square meter of shorebird habitat in a broad-scale unit had the same probability of selection, but no area could be selected more than once per interval. When the program selected a square meter of habitat located within a fine-scale unit that was $\leq$5 ha, the entire fine-scale unit was included in the sample. During the pilot study, we determined fine-scale units >5 ha could not be effectively surveyed during a single visit. Therefore, when a square meter of habitat was selected within a fine-scale unit >5 ha, the 5 ha of habitat nearest to the selected meter was delineated by the program and this area was included in the sample. The program then selected a random fine-scale unit from the sample as a starting point for field surveys. It arranged the remaining fine-scale units along a minimum distance survey route and included a road map of survey locations in the output. The program provided an alternate unit for each selected unit, but alternate units were only surveyed when primary units were unavailable.

We conducted shorebird surveys from a vehicle or on foot, depending on the visibility or location of the fine-scale unit, during daylight hours on randomly chosen dates within an interval. After arriving at a fine-scale unit, the observer waited several minutes before initiating a survey. Each fine-scale unit $\leq$ 1 ha was surveyed for a minimum of five minutes during a visit to standardize sampling effort. We added equal survey time for each additional hectare of habitat surveyed within a fine-scale unit. Shorebirds were observed with a 10 x 60 spotting scope or 8 x 40 binoculars. All shorebirds observed in the fine-scale unit were identified and counted.

To characterize habitat, we estimated percent total cover of shorebird habitat (saturated substrate and shallow water < 16 cm) within each fine-scale unit and further classified each fine-scale unit into one of the following wetland categories: wastewater impoundment, riverine, lacustrine, palustrine and floodwater (Cowardin et al. 1979). For the final analysis, each fine-scale unit was classified into a distinct shorebird habitat type using the combined inundation class and wetland category assignments (i.e. permanent riverine, semi-permanent palustrine, and temporary floodwater). Cover classes for shorebird habitat were: 0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, and >95%. Cover-class midpoints were used in the analysis.

To describe the effect of weather variables on shorebird habitat patterns, we collected daily weather data from ten Oklahoma Mesonet weather stations. The Oklahoma Mesonet program consists of a network of 119 automated observation stations that measure seventeen weather and soil variables several times daily (Oklahoma Climatological Survey 2010). The station closest to the centroid of a broad-scale unit was selected to collect data associated with that unit.

Weather patterns and shorebird habitat

Prior to analyzing these data, we used Spearman rank correlation coefficients to select a subset of non-redundant weather variables among the seventeen weather variables initially collected. We summarized daily weather variables by the survey interval in which they were collected (D23) and by 46 (D46 [interval + preceding interval]) and 69 day (D69 [interval + preceding two intervals]) periods. Weather variables with correlations >0.50 were considered redundant. Among redundant variables, we selected the variable with the strongest correlation with the incidence of shorebird habitat. Estimates of habitat incidence were the proportion of sampled fine-scale units of each habitat type with shorebird habitat present during a survey interval of a broad-scale unit. Data associated with wastewater impoundment habitats were removed from this analysis because anthropogenic management activities, not weather patterns,

were the main cause of variability during the study. Among the shorebird habitat types, average daily temperature, total daily precipitation, average daily wind speed, daily maximum barometric pressure and daily total solar radiation had the strongest relationship with incidence of shorebird habitats.

The direction of the correlations between the shorebird habitat types and selected weather variables were similar within the permanent and temporary inundation classes. Therefore, we pooled wetland categories within these inundation classes for the final analysis. Because inverse correlations existed among wetland categories in the semi-permanent inundation class and the selected weather variables, we split these observations into two corresponding groups for the final analysis. Finally, we examined the correlations between the selected weather variables and the estimates of habitat incidence for each habitat group among time periods. For the final analysis, we summarized each variable over the time period with which it had the strongest correlation with the response.

We used multi linear regression to describe patterns in the incidence of shorebird habitat using the selected weather variables. All data were tested for normality and homogeneity of variance and transformed when necessary. To identify which models best explained observed patterns in habitat incidence for each habitat type, we used an information theoretic framework to compare alternative models (Burnham and Anderson 2002). The alternative models represented all additive combinations of each global model and a null model. We used Akaike's information criterion adjusted for small sample sizes (AICc) to compare the relative ability of alternative models to explain observed patterns. We calculated ΔAICc, Akaike weights (w_i), and model composite parameter estimates across all models in each candidate set to evaluate the support for each model given the data (Burnham and Anderson 2002). We considered all models with a $\Delta AICc < 6$ to have support, but only selected models for the "best models" set when the AICc value for a model was less than the AICc values of all the simpler models within which they were

nested (Richards 2008). R^2 values were also examined to assess the amount of variability explained by individual models.

Shorebird habitat metric

Initially, we used ESRI, ArcGIS 9.0 (1999-2004) GIS software to convert the shorebird habitat layer from vector to raster data. The program converted each 10 m^2 of shorebird habitat within a fine-scale unit polygon into a raster grid cell and assigned each cell to a specified habitat type. Areas not delineated as shorebird habitat were not assigned to any habitat type. A point was placed on each cell located within a fine-scale unit.

We then applied the data to a kernel-density estimation program. Kernel density estimation is a non-parametric analytical technique that generates a smoothed density average for data points over a local neighborhood (Worton 1987, 1989; Seaman and Powell 1996). For each survey interval (n=166), we incorporated the habitat incidence estimates that we calculated for each habitat type into the kernel function. A kernel function of a specified smoothing parameter (*h*) was placed on each point, with the height and thus volume determined by the habitat incidence estimate (*p*) for a given habitat type during an interval. Thus, the density value at distance x from a unit with probability *p* was fn(x) x *p*. This method accounted for the different sizes and spatial arrangement of fine-scale units. Habitat density estimates were calculated with the *h* parameter of the kernel density function set to 500 m, 1 km, 2 km and 3 km for all survey intervals of the study (Fig 1.3a, g-i). Habitat incidence estimates were constant across different values of *h*, and different habitat incidence estimates for each interval were consistent at different values of *h*.

The program assigned a density estimate to each 10m^2 cell within the broad-scale unit. Each raster grid output was displayed as a continuous habitat density surface in the GIS. Habitat density estimates ranged from zero to one. A density value of one equaled complete cover of shorebird habitat at a given scale. The density estimates for each fine-scale unit used in the

analysis was the density value at the centroid of units $\leq$ 5 ha or the centroid of 5 ha survey areas within fine-scale units >5 ha.

Spatial scaling and shorebird occurrence

We used classification tree analysis (CTA) (Breiman et al. 1984) to model the relationship between shorebird occurrence in a fine-scale unit and the habitat density estimates calculated from the different *h* parameter values. We performed this analysis with data from 166 survey intervals collected among the ten broad-scale units. Total habitat area for each fine-scale unit surveyed during the 166 intervals was also calculated and modeled for comparison. We chose CTA because it is appropriate for analyzing complex ecological data with a non-standard data structure, it can detect non-linear responses and complex interactions, and it is robust to outliers (De'ath and Fabricius, 2000).

We built classification trees using the Gini Index, with priors set to equal. We used 10-fold cross validation, repeated 1000 times to smooth the estimated error rates, and then used the 1 – SE rule to select the pruned tree size (Breiman et al. 1984). To evaluate the overall classification tree performance we calculated the correct classification rate (CCR) and chance-corrected classification accuracy statistic (*Kappa*) of each tree. In addition, we derived a *p*-value for each pruned tree using Monte Carlo re-sampling. We created 1,000 trees through random permutation of the data and compared the CCR of our classification trees to the distribution of CCRs.

In addition, we performed a cross validation among the seasons included in this study to test the robustness of the final tree model. Splitting and model selection criteria remained constant for all constructed trees and were the same as those previously described. We first performed separate classification tree analyses on data from each season. We compared the results of these trees to each other to check for possible trends between seasons. The classification trees were similar among seasons and partitioned the data at comparable habitat

density values. Classification trees had an average CCR of 84.2%. We then conducted a five-fold cross validation using each season's observations to predict the response of the other season. The average CCR of the observed vs. predicted was 84.1%. Based on these results, we pooled all season's observations for the final analysis.

As part of our final analysis, we performed a ten-fold cross validation to assess the potential effects of each broad-scale unit on the final model. For this cross validation, we constructed a tree from nine of the ten broad-scale units and used this model to predict the response of the tenth unit and repeated this process ten times. We calculated the CCR of each classification tree and each units' predicted response. Finally, we compared the results among classification trees to assess the influence of each broad-scale unit on the final tree model. All analyses were conducted using R 2.12.1 (R Development Core Team, 2010) and SAS 9.1 (Statistical Analysis System, 2003) software.

RESULTS

We surveyed 14,444 fine-scale units that represented a total area of 26,632 ha during this study. At the time of survey, shorebird habitat was present in 8,337 fine-scale units. We observed shorebirds in 1,321 of the fine-scale units and encountered 29 shorebird species during surveys (Table 1.1).

Weather patterns and shorebird habitat

The most parsimonious multi linear regression models to predict the incidence of shorebird habitat are listed in Table1.2. The variable total daily precipitation (D46) was included in all models among the "best models" set for the response incidence of temporary habitat. The model with the most support given the data and set of candidate models for temporary habitats also contained the variables average total daily solar radiation (D46) and average daily temperature (D23) (w_i = 0.54). This model had 3.2 times more support over the next top model in

the set and explained 33% of the variation in temporary habitat incidence. The incidence of temporary habitat was positively related to increases in total daily precipitation (D46) and negatively related to increases in average daily temperature (D23) and average total daily solar radiation (D46).

The most parsimonious model for the response incidence of semi-permanent floodwater habitat contained the variables total daily precipitation (D69) and average total daily solar radiation (D46). This model explained 22% of the variation in the incidence of semi-permanent floodwater habitat and was 1.3 times more plausible than the model containing only total daily precipitation (D69). Similar to temporary habitats types, semi-permanent floodwater habitat was positively related to increases in total daily precipitation, but over a longer time period (i.e., 69 days), and negatively related to increases in average total daily solar radiation (D46). The incidence of semi-permanent lacustrine, riverine and palustrine habitats was well supported by the model containing the variables total daily precipitation (D69), average total daily solar radiation (D46), average daily wind speed (D69) and average daily temperature (D23) ($w_i = 0.71$). This model explained 23% of the variation in the incidence of these semi-permanent habitat types. Unlike semi-permanent floodwater habitat, the relationship between these habitats and precipitation was negative and these habitats were positively related to increases in solar radiation, temperature and wind speed.

The model containing the variables total daily precipitation (D69), average total daily solar radiation (D46), average daily wind speed (D69) and average daily temperature (D23) explained 32% of the variation in the incidence of permanent shorebird habitat. This model was overwhelmingly supported given the data and candidate model set ($w_i = 0.88$). The incidence of permanent habitats were negatively correlated with increasing precipitation, but positively correlated with increasing temperature, solar irradiation and wind speed.

We demonstrate the relationship between the density of shorebird habitats and weather patterns during the study using a subset of density surfaces calculated for sixteen intervals in two broad-scale units (Fig 1.3). The first broad-scale unit we depict contained both large amounts of potential temporary floodwater habitat in the northern half of the unit and permanent riverine habitat along the central interior (Fig. 1.3a-c). The eastern side of the second broad-scale unit contained a potentially large amount of temporary floodwater habitat, but small amounts of other habitat types (Fig. 1.3e-f). Conditions were wet during fall 2007 in the first unit and during spring 2009 in the second unit. Correspondingly, the surfaces in Figure 1.3 illustrate a sequentially inverse pattern of low and high habitat density in the areas dominated by temporary floodwater habitats during wet periods. When conditions were drier in the first unit during spring 2009, only the permanent riverine habitat feature within the landscape contained areas of high-density habitat (Fig. 1.3a-c). Likewise, when conditions were drier in second unit during fall 2007 and spring 2008, habitat density was low throughout the unit (Fig. 1.3e-f). Similar fluctuations in the distribution of low to high habitat density areas were evident within sequences of density surfaces for other broad-scale units in the study.

Spatial scaling and shorebird occurrence

The results of the classification tree models of fine-scale units occupied versus unoccupied by shorebirds and habitat density calculated using four values for *h* or habitat area are listed in Table 1.3. These results indicated that the strongest relationship between the occurrence of shorebirds in a fine-scale unit and density of shorebird habitat occurred when *h* was set to 2 km for the kernel density estimation. The CCR of the classification tree models were lowest when habitat area was used to explain the occurrence of shorebirds and declined when *h* was set to 3 km in the kernel function.

The pruned classification tree model of occupied versus unoccupied fine-scale units using habitat density with $h = 2$ km correctly classified 7,128 of the 8,337 observations (CCR = 85%, *k*

= 0.57, p = <0.001) (Fig. 1.4). Habitat density initially partitioned the observations into two sub-groups (> 0.06/2 km r^2 and < 0.06/2 km r^2) and then further partitioned the observations at 0.16/2 km r^2. At a lower habitat density (<0.06/2 km r^2), shorebirds occupied only 6% of fine-scale units but this increased to 34% when density was > 0.06/2 km r^2 but < 0.16/2 km r^2. Shorebird occupancy was highest (56%) when habitat density was > 0.16/2 km r^2.

The classification tree models constructed during the ten-fold cross validation among broad-scale units were similar and partitioned the data at comparable habitat density values. The average CCR among trees was 85.2% (range = 70% - 99%). However, the model constructed without data from the broad-scale unit in Alfalfa County had a single partition at the 0.06 /2 km r^2 density value and the CCR for this tree was the lowest (CCR = 70%). This indicates that there was a difference between this broad-scale unit and the others and that the partition at the 0.16 density value was greatly influenced by inclusion of data from this broad-scale unit. This was likely due to the presence of the Salt Plains National Wildlife Refuge in this broad-scale unit, which maintained a relatively high density of shorebird habitat during the entire length of the study. However, the model still correctly predicted 78.9% of the data from this broad-scale unit. The average CCR of the observed vs. predicted was 88.2% among all models. These results indicate that our final model was stable and was capable of predicting the occurrence of shorebirds across our large study area.

DISCUSSION

Our results illustrate the effects of erratic weather patterns on the spatio-temporal distribution of shorebird habitat and provide evidence of spatial dependence in the habitat use-patterns of migratory shorebirds within the continental interior of North America. The interaction of weather patterns and the structure of potential wetland habitat within landscapes controlled the distribution of realized habitat resources and thus, at apposite spatial scales, affected the distribution of migratory shorebirds among landscapes. Although attention has been drawn to the

dynamic and unpredictable nature of wetland resources and its potential effects on the habitat-use patterns of migratory shorebirds within the continental interior (Skagen and Knopf 1993; Skagen 2006; Skagen et al. 2008), we are unaware of any studies that have empirically demonstrated this phenomenon at spatial scales relevant to migratory shorebirds.

The relationship between wetland habitat types and weather patterns is complex. Different wetland types responded conversely to the same weather variables and the strength of the effect of weather patterns on the incidence of wetland habitat types varied with duration. Quantifying the shifting distributions of available shorebird habitat was further complicated by local variation among weather variables and differences in the spatial structure of potential wetland habitat types among landscapes. At any given time within the study area, local and heavy precipitation events created landscapes with extant ephemeral wetland habitats while other landscapes were rendered barren by extended dry conditions. In the case of more permanent wetlands, the extended dry conditions actually enhanced habitats for shorebirds by creating expanses of shorebird habitat along wetland edges. However, these patterns were not mutually exclusive within and among landscapes but rather existed along a gradient and as local weather patterns caused some habitats to dissipate other habitats became available.

Previous investigations of migratory shorebirds in the interior of North America have noted similar trends among ephemeral and semi-permanent wetlands during wet and dry periods (Skagen et al. 2008). In these systems, the highly dynamic nature and shifting distributions of available habitats makes the availability of specific wetlands unpredictable. Several authors have suggested that these shifting and unpredictable habitat patterns have led to the "hop" migration strategy (Piersma 1987) and the opportunistic use of habitats by migratory shorebirds passing through the continental interior (Skagen and Knopf 1993; Warnock et al. 1998; Skagen 2006). Our findings support this view. Many wetlands only provided habitat during portions of the study. Similarly, wetland complexes at broad spatial scales (i.e., 2 km) were limited by the

spatial structure of potential wetland habitat types among landscapes and were transitory because wetland types within complexes responded differently to weather patterns.

Forecasts of climate change underscore the need for baseline data on the response of shorebird habitats to contemporary weather patterns within the Southern Great Plains. Understanding the relationship between weather patterns and ephemeral wetlands within the continental interior is especially important. Ephemeral wetlands are vital to many migratory shorebird species (Skagen et al. 2008) and intrinsic factors associated with finer scale aspects of these wetlands are important to shorebird habitat-use patterns (Davis and Smith 1998; Davis and Smith 2001, Webb et al. 2010). Our results suggest a strong positive relationship between short-term increases in precipitation and the incidence of temporary shorebird habitats. Conversely, increases in temperature and solar radiation negatively impacted the incidence of these habitats. These relationships are alarming when coupled with forecasts of a warmer and drier climate for this region (IPCC 2007). When future climate warming scenarios were applied to wetland landscapes within the prairie pothole region of North America, models predicted substantial reductions in the availability of seasonal wetlands among complexes and indicted these wetlands were the most vulnerable to a warmer and dryer climate (Johnson et al 2010). Our results suggest similar prospects for these wetlands in the Southern Great Plains.

The prevailing theoretical model used to understand the process of stopover selection used by migratory birds implies that migratory birds initially rely on broad-scale cues and progress toward finer-scale characteristics (Hutto 1980; Moore 2000; Petit 2000; Deppe and Rottenberry 2008). However, predictions of a drier and warmer climate for the Southern Great Plains (IPCC 2007) may have important implications at the spatial domain in which migratory shorebirds use broad-scale cues to select habitat within this region. At broad spatial scales, temporary wetlands often played an important role in the formation of complexes of high-density wetland habitat among our study landscapes. Wetland complexes with high-density shorebird

habitat were often complemented by or predominantly composed of temporary wetlands that only became available after wet weather. During dry conditions, high-density habitat was limited to a few large-scale permanent wetlands or was unavailable within landscapes because temporary wetlands were absent from these complexes. In light of current climate projections for this region (IPCC 2007), we recommend future research on the affect of arid scenarios on ephemeral wetlands within the Southern Great Plains. Our results indicate that broad-scale complexes of high-density habitat may provide important cues for migratory birds during the process of habitat selection. However, we suggest that the absence of ephemeral wetlands from complexes may preclude the formation of high-density habitat within many landscapes in a warmer and dryer climate.

Our approach is promising because it produced plausible and detailed broad-scale shorebird-habitat distribution maps that led to a robust and general predictive model. By incorporating temporal variation in the incidence of habitat types within each landscape into the metric, we were able to elucidate actual habitat patterns at different time steps. This approach has an advantage over metrics within existing software programs (i.e., FRAGSTATS 3.2, ArcGIS 9.0) because these programs were only capable of measuring the structure of temporally static habitat patches in spatially explicit data sets. For example, a preliminary analysis of these data using the metric Euclidian nearest neighbor distance (ENN) (McGarigal et al. 2002) showed no relationship between ENN and shorebird occurrence patterns ($r = 0.11$, $p > 0.5$). Contrastingly, our analysis demonstrated strong relationships between shorebird occurrence patterns and habitat configuration at several spatial scales. Furthermore, the explicit integration of spatial scale into the metric allowed for the measurement of habitat density over a range of scales illustrating habitat patterns in both time and space. We recommend similar metrics be developed to measure the shifting distributions of shorebird habitats within other regions of the continental interior to better understand if these patterns vary between different regions and to what extent.

Broad-scale habitat density may be a simple but extremely relevant ecological factor to the distribution of shorebirds during migration. This generalization may be practical for conservation efforts because our model describes the occurrence patterns of migratory shorebirds at a community level. Our results indicate that when shorebirds are modeled collectively, the relationship between shorebird occurrence and habitat density was strongest at the 2 km spatial scale. Optimal foraging theory suggests that a forager will minimize the energetic costs associated with searching for resources to maximize energetic intake (MacArthur and Pianka 1966; Charnov 1976). Consistent with foraging theory, we hypothesize that by selecting broad-scale complexes of high-density wetland habitat shorebirds can use more wetland resources with reduced searching cost. Under these conditions shorebirds have increased access to greater foraging opportunities. Farmer and Parent (1997) came to a similar conclusion when comparing the movements of radio-tagged Pectoral Sandpipers *(Calidris melanotos)* among three landscapes in the Midwestern US. They found that Pectoral Sandpipers moved more frequently for shorter distances among wetlands in landscapes with greater wetland connectivity. Additionally, the mixture of wetland types within complexes may provide a greater range of exploitable niches for species of wetland communities. Several studies have demonstrated an association between increased species richness and intra wetland proximity for various wetland taxa (Wettstein and Schmid 1999; Uchida and Inoue 2010; Ribeiro et al. 2011) including wetland birds (Naugle et al. 1999; Web et al. 2010). Management for complexes of high-density wetland habitat at a 2km scale may better facilitate conservation decisions because it provides a generally applicable management opportunity that can positively affect a range of species with focused conservation resources.

We provide empirical support for ecological scaling techniques that are currently limited despite increased attention (Wheatley and Johnson 2009). Our results indicate that migratory shorebirds exhibit scale-dependent patterns in habitat use within the study area. When we

compared degrees of spatial dependence, habitat density was a better predictor of shorebird occurrence than habitat area and the strength of the relationship between shorebird occurrence and habitat density varied with spatial scale. In addition, when the distance of the scalar argument in the habitat density metric was increased to 3km, the relationship between habitat density and shorebird occurrence declined. This suggests that the 2 km spatial scale represents a maximum beyond which habitat density may no longer influence the habitat-use patterns of shorebirds during a stopover event.

Positive relationships between migratory shorebird species and both patch-level and landscape-level wetland spatial structure have been documented by several other studies in the region (Farmer and Parent 1997; Niemuth et al. 2006; Webb et al. 2010). However, these studies did not examine habitat along a scale continuum to identify potential scale domains where habitat structure was most relevant to the study species. Failure to account for scale-related issues can influence our perceptions of species-habitat relationships and lead to ambiguous and contradictory results among studies (Weins 1989; Cushman and McGarigal 2004b; Li and Wu 2007). In order to develop conservation strategies that operate at the appropriate temporal and spatial scales, there is an urgent need to identify the domains of scale that are relevant to migratory shorebirds within the region (Skagen et al. 2008). We therefore emphasize the importance of using a multi-scale approach to study habitat-use patterns. We further suggest that future research efforts directed at migratory shorebirds within continental interior landscapes integrate our findings into census techniques and monitoring programs.

Our final model predicts shorebird occurrence within a large study area and adds insights into the relationship between shorebirds and habitat density at broad spatial scales. Few fine-scale units were occupied by shorebirds when habitat density was < 0.06/2 km r^2, even though 72.5% of the total units surveyed were at low density. When habitat density was >0.06/ 2 km r^2, shorebirds where 5.7 times more likely to occupy a habitat patch, and occupancy was 9.3 times

more likely when habitat density was > 0.16/2 km r^2. The final model predictions were quite good and robust. We attribute this to the capacity of the metric to measure the shifting distributions of habitat density among spatial scales. Additionally, by selecting the measurement of the habitat density variable at the most ecologically relevant scale, we optimized the accuracy and explanatory power of the model. The high predictive capability and robustness of the 2 km model suggests that this method may provide an accurate measure of spatiotemporal dynamics in habitat structure at a spatial domain in which migratory shorebirds use broad-scale cues to select habitat.

Conservation and management of migratory shorebird stopover habitats should aim to provide areas of potentially high-density habitat at a 2 km spatial scale. To preserve an adequate network of stopover resources we must integrate scaling principles into research to identify the spatial and temporal scales relevant to shorebird-habitat relationship during migration. We need to recognize the importance of both spatial and temporal dynamics within and among the wetland complexes of a migration stopover network. Wetland complexes that include a diverse mixture of different wetland types and inundation periods may best ensure that at least some adequate stopover resources are persistently present within this continually changing landscape.

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Table 1.1. List of migratory shorebird species and migration period during which each species were encountered within shorebird habitat units located in north-central Oklahoma, US, 2007-2009. Shorebird habitat was defined as shallow water (< 16cm) and saturated substrate within and surrounding wetlands.

Species	Spring	Fall
Black-bellied Plover *(Pluvialis squatarola)*	X	X
American Golden-Plover *(Pluvialis dominica)*	X	X
Semipalmated Plover *(Charadrius semipalmatus)*	X	X
American Avocet *(Recurvirostra americana)*	X	X
Black-necked Stilt *(Himantopus mexicanus)*	X	X
Willet *(Tringa semipalmata)*	X	X
Lesser Yellowlegs *(Tringa flavipes)*	X	X
Greater Yellowlegs *(Tringa melanoleuca)*	X	X
Solitary Sandpiper *(Tringa solitaria)*	X	X
Whimbrel *(Numenius phaeopus)*	X	
Long-billed Curlew *(Numenius americanus)*	X	
Hudsonian Godwit *(Limosa haemastica)*	X	
Marbled Godwit *(Limosa fedoa)*	X	X
Ruddy Turnstone *(Arenaria interpres)*	X	X
Red Knot *(Calidris canutus)*		X
Sanderling *(Calidris alba)*	X	X
Dunlin *(Calidris alpina)*	X	
Semipalmated Sandpiper *(Calidris pusilla)*	X	X
Western Sandpiper *(Calidris mauri)*	X	X
Least Sandpiper *(Calidris minutilla)*	X	X
White-rumped Sandpiper *(Calidris fuscicollis)*	X	
Pectoral Sandpiper *(Calidris melanotos)*	X	X
Baird's Sandpiper *(Calidris bairdii)*	X	X
Buff-breasted Sandpiper *(Tryngites subruficollis)*	X	X
Long-billed Dowitcher *(Limnodromus scolopaceus)*	X	X
Wilson Snipe *(Gallinago delicate)*	X	X
Stilt Sandpiper *(Calidris himantopus)*	X	X
Wilson's Phalarope *(Phalaropus tricolor)*	X	X
Red-necked Phalarope *(Phalaropus lobatus)*	X	X

Table 1.2. Minimum AICc (ΔAICc < 6 [a]) models, Akaike weights (w_i) and r^2 statistics for the incidence of shorebird habitat classes in ten landscapes within north-central Oklahoma, US, 2007-2009. Standardized composite model parameter estimates for the explanatory variables in the top model sets are included. The number of days over which explanatory variables were summarized are noted in parentheses.

Habitat Class	Candidate Models	ΔAIC_c	w_i	r^2	Standardized coefficient
Temporary	Average daily temperature (23)	0	0.54	0.33	-0.19
	Total daily precipitation (46)				+0.58
	Average total daily solar radiation (46)				-0.30
	Total daily precipitation (46)	1.7	0.17	0.30	
	Average total daily solar radiation (46)				
	Total precipitation (46)	5.6	0.03	0.29	
Semi-permanent	Total daily precipitation (69)	0	0.34	0.22	+0.41
Floodwater	Average total daily solar radiation (46)				-0.14
	Total daily precipitation (69)	0.4	0.27	0.21	
Semi-permanent	Average daily temperature (23)	0	0.71	0.23	+0.66
Palustrine	Total daily precipitation (69)				-0.17
Lacustrine	Average total daily solar radiation (46)				+0.50
Riverine	Average daily wind speed (69)				+0.54
Permanent	Average daily temperature (23)	0	0.88	0.32	+0.52
	Total daily precipitation (69)				-0.48
	Average total daily solar radiation (46)				+0.27
	Average daily wind speed (69)				+0.39

[a] Alternative candidate models were only selected for the "best model" sets when the AICc value for a model was less than the AICc values of all the simpler models within which they were nested (Richards 2008).

[b] Habitat types within the semi-permanent habitat class were split into two groups for the analysis. Habitat types included in each group are listed in italics.

Table 1.3. Results of classification tree analysis comparing models of the relationship between shorebird occurrence and habitat area or density of fine-scale units. Habitat density estimates were calculated using habitat incidence probability estimates from field data and 500 m, 1 km, 2 km and 3 km for the *h* parameter in a kernel density estimation function. All models were significant, but the 2 km habitat density model had the highest correct classification and chance corrected classification statistic (*Kappa*).

Variable	Correct classification rate	*Kappa*	*P*
Habitat area	56%	0.13	<0.0001
500m	71%	0.41	<0.0001
1 km	74%	0.49	<0.0001
2 km	85%	0.57	<0.0001
3 km	66%	0.32	<0.0001

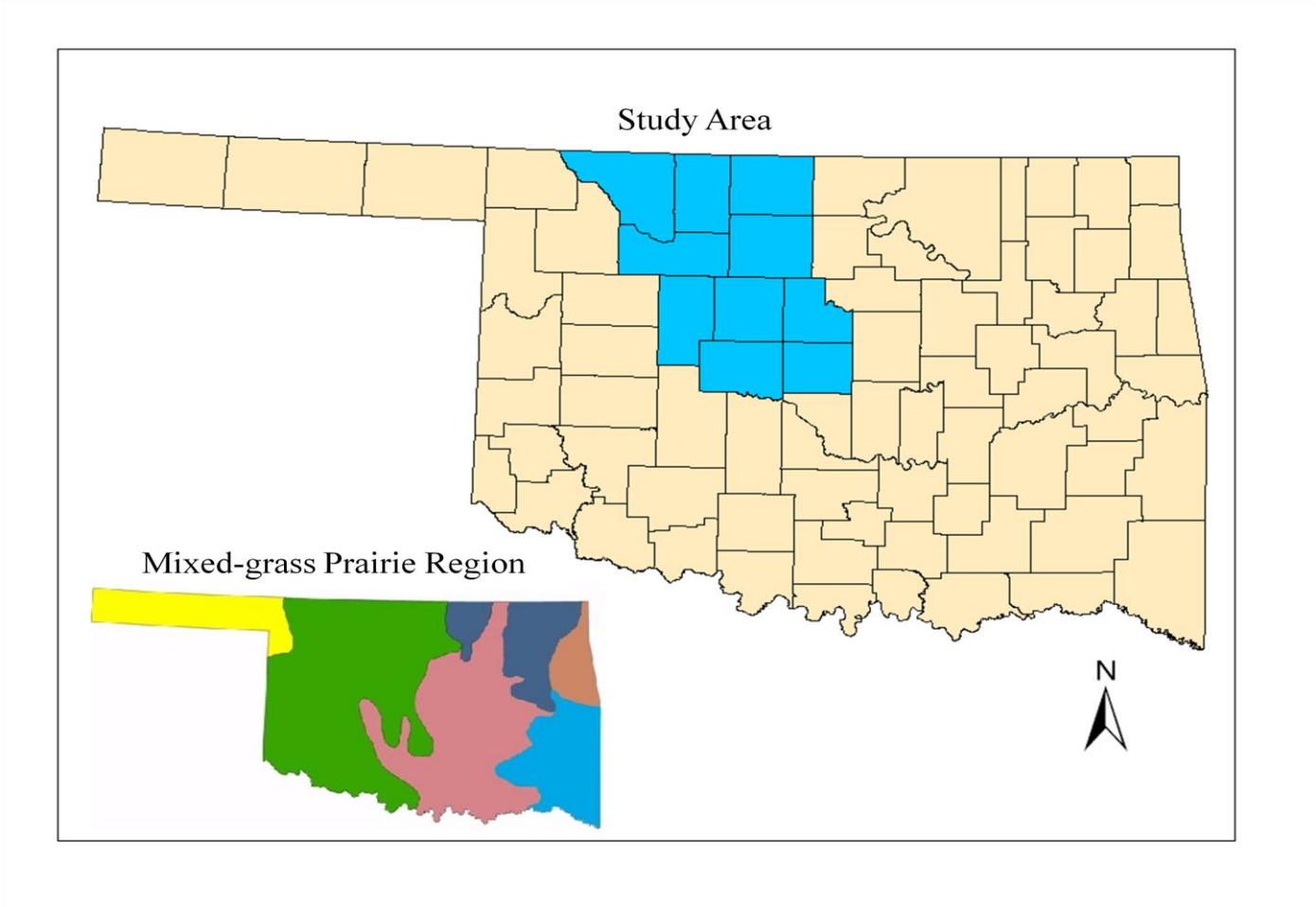

Figure 1.1. The study area is indicated by the blue counties within the map of Oklahoma, US. The location of the mixed-grass prairie region is indicated by green in the inset image. The study area encompassed Alfalfa, Blaine, Canadian, Garfield, Grant, Kingfisher, Logan, Major, Oklahoma, and Woods counties.

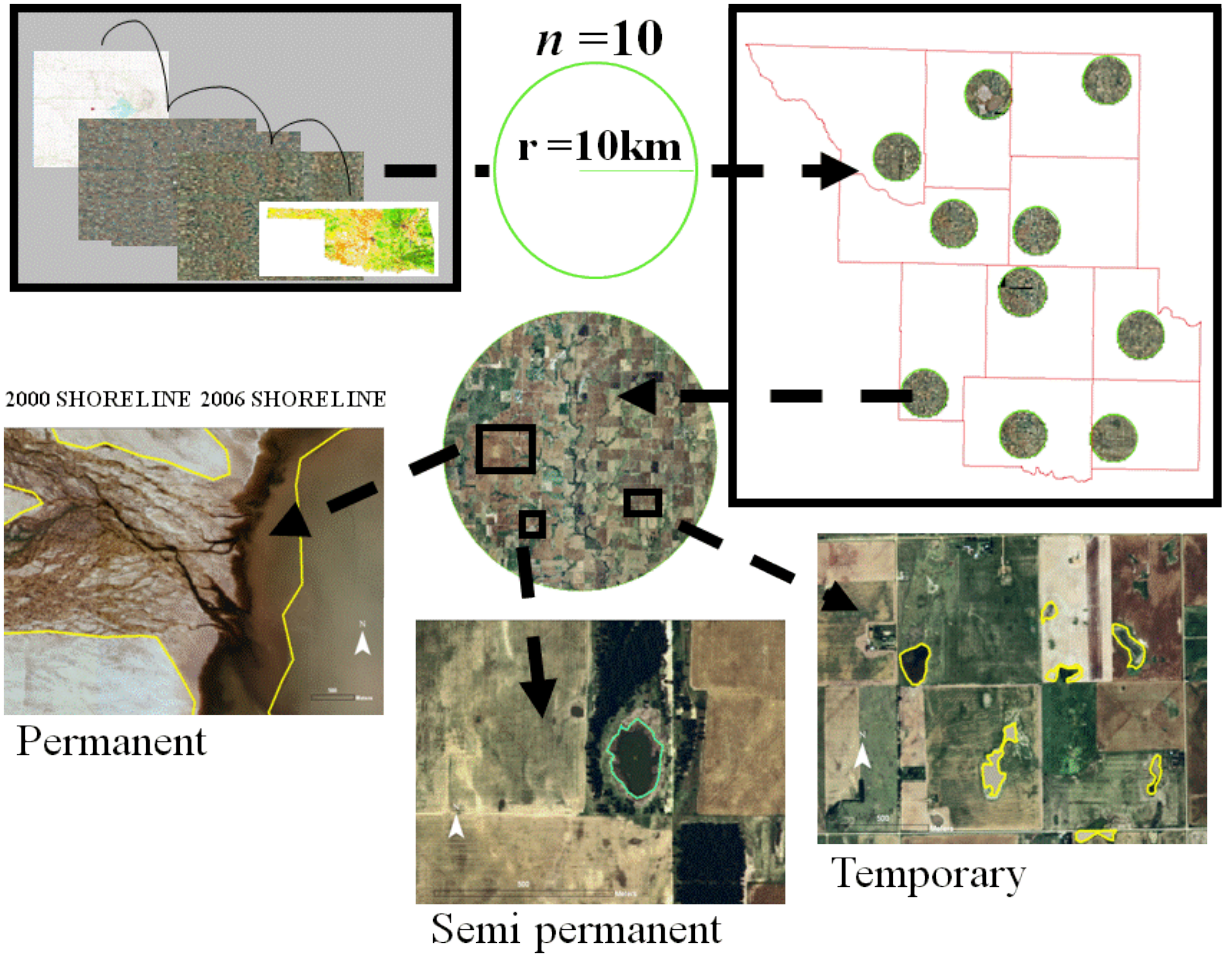

Figure 1.2. A graphical model depicting the acquisition and assemblage of the base data layers, the placement of broad-scale units within the study area, and the examination of broad-scale units for shorebird habitat. All identified shorebird habitat was delineated as a discrete polygon and then classified into one of the three habitat inundation classes shown.

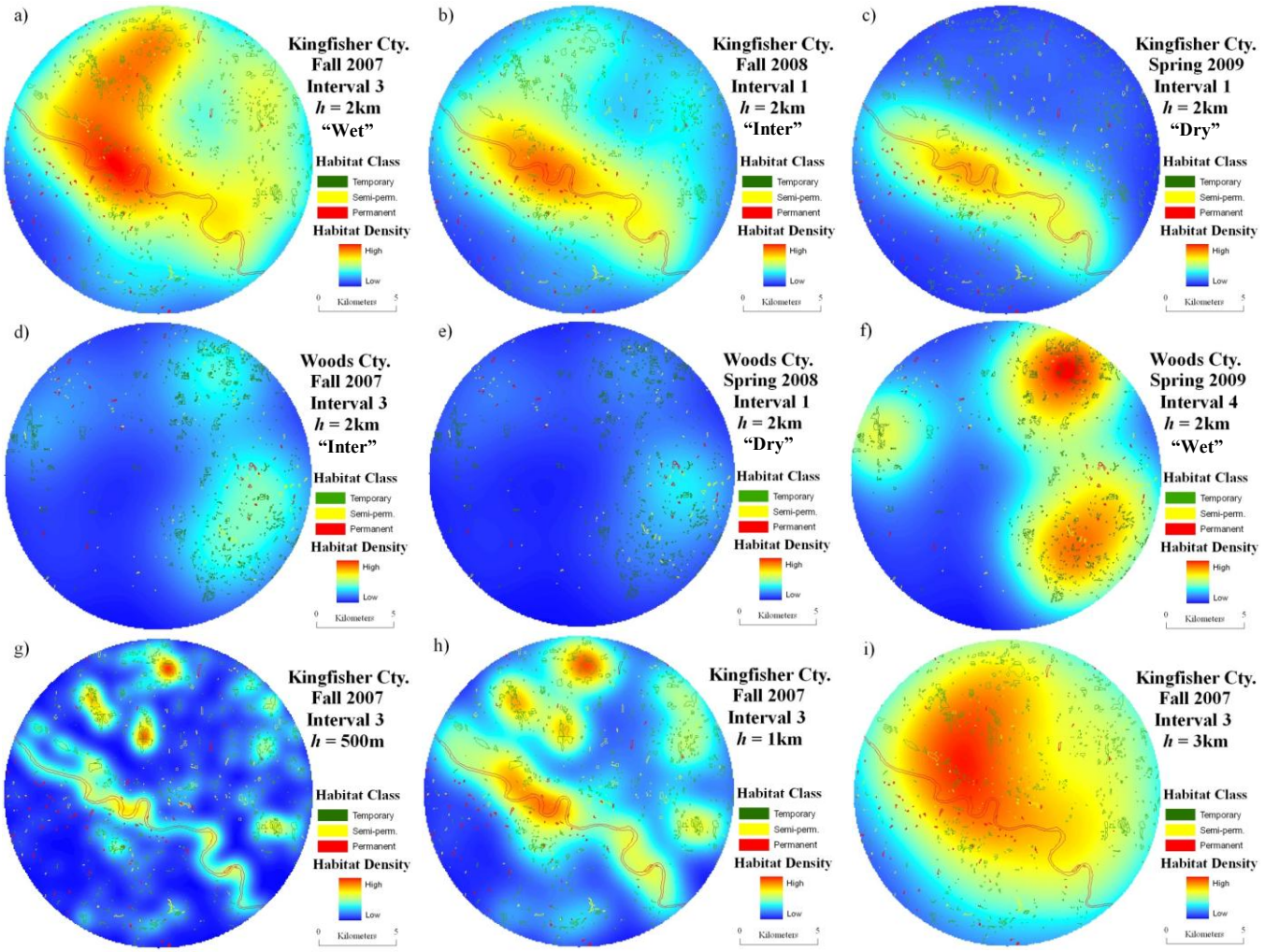

Figure 1.3. Images a thru f show habitat density surfaces calculated using habitat incidence (*p*) estimates collected in the study area and kernel density estimation. Habitat (*p)* estimates were the proportion of sampled fine-scale units of a habitat type with

habitat present during a survey interval of a broad-scale unit. The *h* parameter was held constant (*h* = 2 km). A sample of three of the sixteen surfaces produced for each of two different broad-scale units (images a thru c and d thru f, respectively) are shown in sequence from spring 2007 thru spring 2009. The general conditions are noted as wet, dry or intermediate (inter) in each image legend. Images a and g thru i show habitat density surfaces calculated with habitat *p* estimates held constant and the *h* parameter varied (*h* = 2km, 500m, 1km, and 3km, respectively). Shorebird habitat is outlined and displayed by class on each surface.

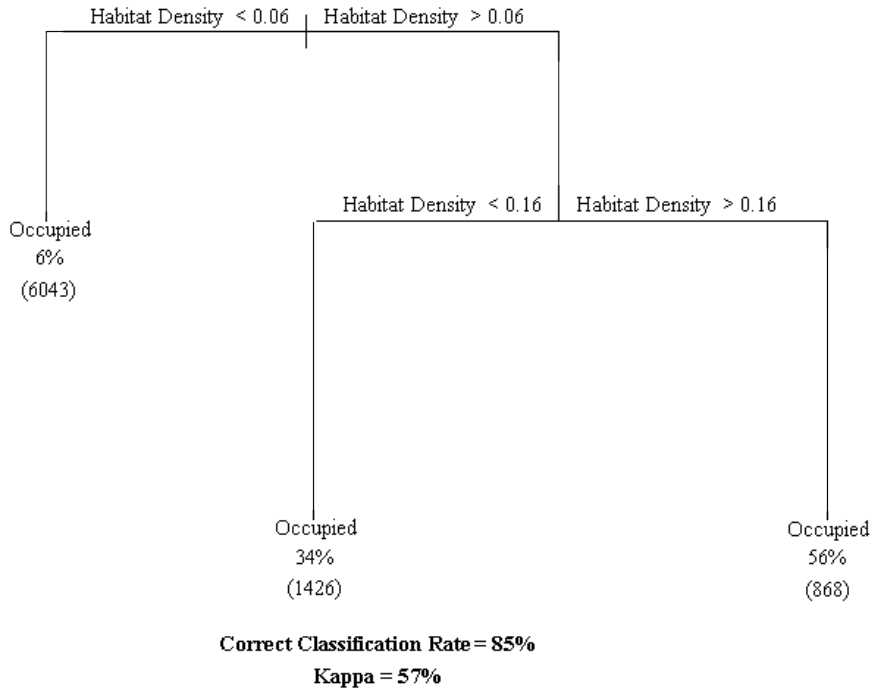

Figure 1.4. Pruned classification tree model for the categorical response variable of fine-scale sampling units occupied vs. unoccupied by migratory shorebirds. The explanatory variable shorebird habitat density was calculated using kernel density estimation. Habitat probability estimates collected during each survey interval of a broad-scale unit during the study were incorporated into the kernel function and the *h* parameter for the function was set to 2 km. The density value at the centroid of each sampled fine-scale unit was used in the analysis. Each partition in the classification tree is labeled with the splitting rule. A habitat density value of 1.0/2 km r^2 would equal complete shorebird habitat cover. Each terminal node is labeled with the proportion of observations within the occupied category. The total number of observations in the terminal group is given in parentheses.

CHAPTER II

BROAD-SCALE RELATIONSHIPS BETWEEN SHOREBIRDS AND LANDSCAPES IN THE SOUTHERN GREAT PLAINS

ABSTRACT

It is well established that patch-level habitat characteristics affect the use of stopover sites by migrating shorebirds, however, it is also essential to assess the broad-scale factors that influence the use of stopover habitat. We conducted surveys of ten 10-km radius landscapes in north-central Oklahoma from 2007 thru 2009 to determine how the composition of wetland habitats and peripheral land cover types influence shorebird diversity and abundance during migration. We categorized wetland habitats by inundation period and wetland type. We used generalized linear modeling and an information theoretic framework to identify the models and wetland habitats that best explained the observed abundance and diversity patterns of five different shorebird groups, which we based on breeding status and migration distance. We found that migratory shorebird abundance and diversity increased with the wetland habitat within the landscape regardless of the amount of other semi natural and developed land cover. Furthermore, the response of shorebirds to the landscape composition of different wetland types varied with migration distance and breeding status. Generally, the landscape area of riverine and ephemeral floodwater habitats were important predictors of migratory shorebird abundance and species richness. Abundant ephemeral floodwater habitats were particularly important to intermediate and long distant migrant shorebird abundance and diversity. We conclude that landscape-level studies can

provide important additional insights on the en route habitat use of migratory shorebirds. We recommend that conservation priority be given to landscapes that include abundant riverine habitats with a large compliment of potential ephemeral floodwater habitats.

Key words: Avian migration, landscape composition, landscape ecology, habitat use, prairie wetlands, stopover, wetland complex.

INTRODUCTION

Nearly half of the shorebird species in North America are considered to be in decline (Brown et al. 2001; Morrison et al. 2001) and of the shorebird populations with known trends, nearly 50% may be declining worldwide (Wetlands International 2002; Stroud 2003). Concerns over these apparent declines have led to research to identify possible causes on breeding and wintering grounds (Jehl and Lin 2001; Morrison et al. 2004), but recent studies have suggested that population limitation may also occur during migration (Baker et al. 2004; Morrison 2006). For shorebirds that migrate through the interior of North America, research indicates that these birds may be more vulnerable to decline than oceanic or coastal migrants because of intrinsic factors associated with a transcontinental migration strategy (Thomas et al. 2006). Moreover, many interior shorebird migrants depend on a wide variety of wetlands that have experienced extensive losses (Dahl and Allord 1996), and these wetlands are predominantly outside of established preserve networks (Skagen et al. 2008). These factors combined with a lack of legal protection for isolated wetlands throughout the interior of North America (Haukos and Smith 2003; van der Valk and Pederson 2003) and forecasts of pervasive land transformation through agricultural intensification and climate change (Tilman et al. 2001; IPCC 2007) emphasize recent conservation concerns directed at shorebirds that migrate through the interior of North America (Skagen 2006).

Within the interior of North America, many migrating shorebirds predominantly forage in exposed mud and shallow water habitats that occur within a variety of wetland types (Skagen and Knopf 1993; Skagen et al. 2005; Colwell 2010). The use of interior wetlands by different species of migrating shorebirds is influenced by habitat characteristics such as water depth, prey availability, amount of mudflat and shallow water habitat, and vegetation height and cover (Davis and Smith 1998). Moreover, shorebird foraging niches are defined by multiple dimensions that include morphological characteristics, diet diversity, prey size, and foraging methods which simultaneously act together to segregate migrating species at stopover sites (Davis and Smith 2001). Thus, differences among wetland habitat characteristics influence the diversity and abundance of migrating shorebirds among wetland stopover sites (Skagen and Knopf 1994; Webb et al 2010a). Additionally, other factors such as migration strategy and the distance traveled between breeding and wintering grounds may influence the habitat-use patterns of shorebirds during migration. For example, shorebirds that travel shorter distances between successive stopover areas tend to accumulate smaller fuel loads and have shorter residency periods (i.e., hours to days) at stopovers than those species that travel longer distances between refueling stops (Piersma 1987; Warnock 2010). These movement and stopover strategies vary among and within species with the predictability and availability of different wetland resources along migration routes (Piersma 2007, Warnock 2010). Meeting the en route habitat requirements of a complete migratory shorebird community will require information on how the availability of different wetland resources influences species diversity and abundance.

The suitability of a wetland for migrating shorebirds is not solely dependent on the habitat conditions within the wetland, but rather the density of wetland habitats in the surrounding landscape may best explain the distribution patterns among migratory shorebird species that rely on wetlands (Albanese 2011). These complexes of wetlands provide critical resources for many shorebirds traversing the interior of North America (Skagen and Knopf 1994; Skagen 2006).

Although, vagarious annual and seasonal weather patterns cause wide spatio-temporal variation in the distribution of wetland resources available to migrating shorebirds within the region (Skagen et al. 2008; Albanese 2011). Extended dry conditions may preclude availability of ephemeral wetland habitats while exposing habitats along permanent wetland edges. Wet weather patterns provide ephemeral wetlands, but may flood the deeper basins of more permanent wetlands thereby limiting their accessibility as feeding habitat. At broad spatial scales, this inverse pattern exists along a continuum and as local weather patterns cause some habitats to dissipate, other habitats become available. Shorebirds migrating through interior North America appear to have responded to this pattern by being broadly dispersed and relying on opportunistic habitat use (Skagen and Knopf 1993; Skagen et al. 2008).

One of the most consistent patterns in nature is the positive relationship between area, habitat diversity and species richness. Consequently, it is logical that researchers often recommend that conservation efforts must maintain a diverse assemblage of wetlands within complexes to accommodate the diversity of migrant shorebirds that may occur in the region (Skagen et al. 1997; Niemuth et al. 2006; Webb et al. 2010a). This strategy assumes that by maintaining a variety of wetland types with different hydrological conditions, some wetland habitat will be consistently available within complexes such that the interspecific niche requirements of a wide variety of species can be accommodated. However, few studies have provided empirical support for this assumption at the broad scales necessary to examine wide ranging migratory shorebird populations. Furthermore, avian habitat-use patterns during migration may not only depend on the composition of the focal habitat type, but also on the composition of the peripheral land cover types (e.g., area of developed land cover) present within the landscape (Flather and Sauer 1996). Research has suggested that the amount of different land cover types surrounding a wetland may affect its use by migrant shorebirds (Skagen et al. 2005).

The importance of determining the influence of broad-scale habitat availability to migratory birds has been recognized for some time, but empirical support is still lacking (Hutto 1985; Farmer and Weins 1998; Moore 2000). This gap in understanding is consistent among many migratory bird species and suggests an overestimation of the significance of fine-scale factors (Buler et al. 2007). Moreover, to study the influence of landscape-level characteristics on the habitat-use patterns of migratory birds we must adopt accurate study designs (Wheatley and Johnson 2009) and measure landscape variables at scales appropriate to this wide-ranging life history stage (Addicott et al 1987; Wiens 1989). Inclusion of landscape characteristics have improved or solely explained the abundance and diversity of breeding and wintering birds (Pearson 1993; Bolger et al. 1997; Cushman and McGarigal 2003), and for migratory landbirds, empirical support indicating the importance of broad-scale factors has begun to accumulate (Buler et al. 2007). For shorebirds migrating through midcontinental North America, the composition or configuration of wetland habitat measured from a focal patch over broad scales (i.e. landscape context variables) has influenced the within patch occurrence patterns of some species (Farmer and Parent 1997; Neimuth et al. 2006). Studies that use landscapes as the units of study should provide further insights into landscape influences on shorebird species during migration.

Conservation strategies directed at migrant shorebirds, especially those migrating through the interior of North America, require the identification of broad-scale factors that influence en route habitat use (Skagen et al. 2005, 2008). The shifting distributions of wetland habitats and shorebirds have made assessments of broad-scale habitat associations challenging and understanding the use of different wetland habitats difficult. Consequently, conservation strategies for shorebirds are limited without broad-scale quantitative information on how these species respond to changing landscapes and the availability of different wetland types. In this study, we examined the relationship between migrant shorebird abundance and diversity and the

landscape composition of saturated and shallow water habitats and other land cover types present in north-central Oklahoma. Specifically, our objectives were to: (1) identify potential wetland shorebird habitat and use successive habitat surveys to estimate the changing availability of these habitats within landscapes over time, (2) quantify the composition of semi- natural and developed land cover types that were not defined as potential wetland shorebird habitat within landscapes, and (3) examine landscape-level relationships between the diversity and abundance of different shorebird groups and the landscape composition of different wetland shorebird habitats and non habitat land cover types. Our expectations were that the abundance and diversity of shorebirds during migration would be positively related to the area of wetland habitat within landscapes regardless of the composition of other land cover types and relationships with wetland habitat types would differ among shorebird groups.

METHODS

Study area

The study area encompassed 24,372 km^2 of north-central Oklahoma, US and was characterized by intensively managed agricultural areas, grasslands, small forests stands, and broadly distributed urban and suburban developments (Fig. 2.1a). Wetlands within the study area included a range of hydroperiods and types from more permanent lacustrine and riverine wetlands to ephemeral palustrine wetlands and agricultural sheetwater. Erratic and extreme seasonal and annual weather patterns characterize the region causing the distribution and extent of wetlands to vary widely in both space and time (Albanese 2011). The average monthly temperature and precipitation totals across the study area during the three spring study periods was 14.4 °C and 10.1 cm (long-term averages: 14.4 °C and 8.9 cm), respectively, and during the two fall study periods was 23.0 °C and 8.8 cm (long-term averages: 23.4 °C and 7.4 cm), respectively (Oklahoma Climatological Survey 2011).

Experimental design

Our research focused on migrant shorebirds in two suborders, *Scolopaci* and *Charadrii*. During spring, the shorebird migration period within the study area typically begins during late February and ends in early June, while the fall migration period begins in mid-July and ends in October. Accordingly, we conducted this study during five consecutive spring (March − May) and fall (mid July − October) migration periods from 2007 − 2009. Although some shorebird species use dry upland habitat types to forage during migration, we restricted our research to wetland habitats and to those shorebird species that predominately use wetland habitats to forage during migration.

We randomly placed ten, 10-km radius circles (hereafter, landscapes) throughout the entire study area (Fig. 2.1a). We chose the 10-km radius because > 90% of known foraging flight distances in the region were < 10 km (Farmer and Parent 1997). In addition, landscapes of this size encompassed the spatial scales at which the regional migratory shorebird community had the strongest relationship with wetland habitat composition and configuration (Albanese 2011). Finally, the land cover and shorebird habitat present among landscapes were representative of those that characterized the entire study area (Fig. 2.1a) and included a wide range in the amount of land cover and wetland habitat types (Table 2.1). We estimated a sample size of ten landscapes would be required to detect an effect in shorebird abundance using an *a priori* regression power analysis for sample size ($\alpha = 0.05$, $1\text{-}\beta = 0.90$; Lenth 2006) with variance and effect size estimates from pilot study data.

Quantifying landscape composition and shorebird habitat

We quantified the area of potential shorebird habitat within each landscape by combining two methods. Initially, we used Environmental Systems Research Institute's (ESRI) ArcGIS 9.0 (1999-2004) GIS software to assemble 1.0 m resolution 1:12,000 digital ortho-image quarter quadrangles (DOQQs) from 2000, 2003-2006, and 2008. Because our research interests only included shorebird species associated with wetland habitat during migration, we restricted our

definition of shorebird habitat to areas that potentially contain saturated substrate and shallow water (< 16 cm) within wetlands and around wetland edges. Using long-term weather data summaries collected from ten automated weather stations located within or near each landscape (Oklahoma Climatological Survey 2011) and visual assessments of all DOQQs, we classified shorebird wetland habitat into permanent, semi-permanent, and temporary habitat inundation classes. Temporary, semi-permanent, and permanent classes were defined as habitat present only during wet years, not present in at least one dry year, and present in all years from 2000 to 2009, respectively. Although data varied among landscapes, below average precipitation and less wetland habitat characterized the 2004, 2005 and 2006 images, while above average precipitation and abundant wetland habitat characterized 2000, 2003, and 2008 images (Oklahoma Climatological Survey 2011). Within each landscape, we visually examined the entire extent of each DOQQ within the annual series at a 1:10,000 scale. When we located a discrete patch of potential habitat, we delineated the broadest extent of habitat that we could identify among the DOQQs as a polygon. We assigned each discrete patch to an inundation class and to one of the following categories: wastewater impoundment, riverine wetland, lacustrine wetland, palustrine wetland and floodwater (Cowardin et al. 1979) (Fig. 2.1e-f). Because of logistical limitations, we did not delineate habitat patches that never exceeded 1000 m^2 or areas within channelized wetlands that did not exceed 30 m in width among DOQQs. To refine our habitat delineations, we then conducted field surveys of each landscape using $1m^2$ color ortho images of each landscape and of each habitat patch. Maps were marked with UTM grid lines and were used in conjunction with GPS receivers. We surveyed 26,633 ha of shorebird habitat during surveys. Refinements and new habitat patches identified during surveys were continuously updated in the GIS.

The area covered by different land cover types within each landscape was quantified using 2001 National Land Cover Data (NLCD 2001) (Vogleman et al. 2001). Fifteen land cover

subclasses were present within the study area. Using ArcGIS 9.0 (1999-2004) GIS software, we combined subclasses that were defined by the same dominant land cover types (Vogelmann et al. 2001) into six classes. We then used the software program FRAGSTATS (McGarigal et al. 2002) to quantify the total area of each land cover class within landscapes (Table 2.1). For our final analysis, we further combined the six land cover classes into two final classes based on the level of anthropogenic activity associated with each class. The urban/suburban and row cropland classes were combined to form the developed class and the barren, forest/shrubland, grassland/pasture and wetland classes were combined to form the semi-natural class (Fig. 2.1b-d, Table 2.1).

Shorebird surveys

We grouped the shorebird species we encountered during field surveys based on breeding and migratory status within the study area. Migratory species were those species that migrate through and do not typically breed within the study area. Resident species were those species that migrant through but also commonly breed in the study area. In addition, we used data on the migration distances traveled by shorebird species available according to Skagen and Knopf (1993) to assign species to short, intermediate or long distant migrant groups. Table 2.2 contains the group assignment of each species used in our analysis.

Existing data on known residency periods for midcontinental shorebirds during a stopover event suggests a maximum average residency period of 10.5 days (Skagen and Knopf 1994; Farmer and Durbian 2006; Skagen et al. 2008). Accordingly, we assumed that separating our surveys bouts within landscapes by > 10.5 days would ensure independence among our survey data. Therefore, we divided each spring and fall migration period into four 23-day survey intervals. Survey dates for each landscape were randomly selected prior to each interval. We surveyed 13-15% of the total area of potential shorebird habitat within each landscape once during each survey interval. Within each landscape, the proportion of the area sampled in each

habitat inundation class was equal to the proportion of the total habitat area within the landscape that each inundation class encompassed. We estimated a sample size of 13% of the total potential shorebird habitat area within each landscape would be required to detect an effect in shorebird abundance using an *a priori* regression power analysis (Lenth 2006) for sample size ($\alpha = 0.05$, $1-\beta = 0.95$) with variance and effect size estimates from pilot study data.

We developed a software program that randomly selected (without replacement) the required area sample of each habitat inundation class in each landscape at each survey interval. When a square meter of habitat was selected within a habitat patch < 5 ha, the entire area of the patch was included in the sample. However, during a pilot study, we concluded that discrete habitat patches > 5 ha could not be effectively surveyed during a single visit. Therefore, when a square meter of habitat was selected within a habitat patch > 5 ha, the nearest 5 ha of habitat to the selected meter was delineated by the program and this area was included in the sample. Alternates for each selected habitat patch were also chosen if logistical constraints prevented a survey of a selected patch. The program selected a random starting location and arranged the selected habitat patches along a minimum distance survey route. The program also provided a road map with selected and alternate patch locations and individual maps with UTM coordinates for each patch within the landscape.

Shorebird surveys were conducted during daylight hours from a vehicle or on foot, depending on the visibility or location of the habitat patch. After arriving at a habitat patch, we waited several minutes before initiating a survey. First, we recorded the presence or absence of shorebird habitat within the patch. Habitat was considered absent if habitat patches were completely dry or if they were completely inundated with water > 16 cm in depth. If habitat was present, the patch was surveyed for shorebirds. Each habitat patch $\leq$ 1 ha was surveyed for a minimum of five minutes during a visit and equal time was added for each additional hectare of

habitat. Shorebirds were observed with a 10 x 60 spotting scope or 8 x 40 binoculars. All shorebirds observed in a habitat patch were identified and counted.

Statistical analysis

All analyses were performed using R 2.12.1 software (R Development Core Team 2010). All data were tested for normality and homogeneity of variance and transformed when necessary. Logarithmic transformations were used successfully to achieve homogeneity of variance and normal distributions for species abundance, richness and habitat and land cover data (Quinn and Keough 2002). All parameter values in tables and text are untransformed.

We used multi linear regression to assess the relationship between the total abundance and species richness of migratory shorebirds observed during the study and the total area of shorebird habitat, developed land cover and semi-natural land cover within each landscape. For the variable total shorebird habitat area, we used field data to calculate the proportion of each habitat class and category with habitat present during each survey interval in a landscape. We multiplied these probabilities by the total potential area of each habitat type within each landscape. We summed these values to estimate the total habitat area present within each landscape during each interval. For the final analysis, we used the mean of these estimates across all survey intervals in each landscape.

We used linear time-series regression models (Ives and Zhu 2006) to examine the relationship between the abundance and species richness of shorebirds in each response group (i.e., migratory, resident and short, intermediate and long distant migrant shorebird groups) and the area of different shorebird habitats among intervals within landscapes. For each landscape, we used the same methods as described above to estimate the area of habitat present. However, we used estimates for each habitat class and category during each interval in our final analysis. We also calculated the abundance and species richness of shorebirds in each response group during each corresponding interval. For each response group, we constructed global additive

models using the landscape area of habitat within each inundation class (i.e., permanent, semi-permanent, and temporary), the area of habitat within each wetland category by class (i.e., permanent lacustrine, permanent riverine, and permanent palustrine) and the area of habitat among all classes and categories (i.e., permanent riverine and semi-permanent palustrine).

If autocorrelation among observations is ignored, regression analysis is likely to produce biased parameter estimates and detect weak and spurious results (Hoeting 2009; Zuur et al.2009). To test for spatiotemporal autocorrelation among these data, we first fitted each global model with no correlation structure. We examined plots of normalized residuals versus time for each landscape time-series and the correlation coefficients between residuals among landscape time-series (Zuur et al. 2009). Correlation coefficients between residuals among landscape time-series did not indicate spatial correlation among landscapes however, temporal correlation within landscape time-series was apparent. We therefore fitted global models with ordered and moving average autoregressive structures (AR (1) and ARMA, respectively) (Ives and Zhu 2006; Zuur et al. 2009), and compared models using the second order variant of Akaike's information criterion (AIC_c) (Burnham and Anderson 2002). The models with the AR (1) structure consistently eliminated evidence of temporal autocorrelation among residuals and had the lowest AICc value among models. Consequently, we used the AR (1) structure and maximum likelihood estimation to estimate model parameters in the final analysis. This approach accounted for correlation in each habitat variable among sequential surveys within landscapes, where a given habitat area at time (t) was dependent on the given habitat area at (t - 1). For each time-series, we used subsequent observed values to estimate habitat area values for t(0) (Box et al. 1994). The fit of all global models to the data was assessed using residual deviance goodness-of- fit tests.

To identify which models best explained observed patterns in the abundance and richness of shorebirds, we used an information theoretic framework to compare alternative models (Burnham and Anderson 2002). We used AIC_c to compare the relative ability of alternative

models to explain observed patterns. The alternative models represented all additive combinations of each global model and a null model. We calculated the ΔAIC_c and the Akaike weight of each model in the set to evaluate models and to select the most parsimonious models among the candidate set. We considered all models with a $\Delta AIC_c < 6$ to have support, but only selected models when the AIC_c value for a model was less than the AIC_c values of all the simpler models within which they were nested (Richards 2008). We also used the Akaike weights to calculate composite model parameter estimates and summed Akaike weights for each parameter in the "best model" set (Burnham and Anderson 2002).

RESULTS

Using the combination of field surveys and GIS analysis, we delineated and classified 11,733 ha of potential shorebird habitat among landscapes. Within landscapes, an average of 11% (SD ± 7.0%) of the total potential area of shorebird habitat initially delineated in the GIS was corrected using data from field surveys. The land cover analysis revealed relatively similar values in the mean area of developed and semi-natural land cover types, but a wide range in the area of developed and semi-natural land cover types and potential shorebird habitat among landscapes (Table 2.1). During the entire study, habitat was present at the time of a survey in 58% of the potential habitat patches that were surveyed. Among landscapes, the permanent inundation class provided the highest mean area of shorebird habitat, but also had the highest variance among landscapes (Table 2.3). The semi-permanent and temporary inundation classes were similar with respect to the mean area of habitat available. The proportion of surveyed habitat patches with habitat present during a visit was highest for permanent riverine and semi-permanent palustrine and floodwater and lowest for permanent lacustrine, semi-permanent wastewater impoundments and temporary palustrine categories.

Over the entire study, we observed 44,266 shorebirds that included 32 species. Shorebirds were present in all landscapes, however the abundance and richness of shorebirds was

variable among landscapes (Table 2.4). We observed 6,644 individuals of species that commonly breed within the study area (i.e., resident breeders). Among migratory species, intermediate and long distance migrants were the most abundant (n = 23,199, n = 12,253, respectively).

Land cover analysis

The most parsimonious linear regression models to predict the abundance and species richness of migratory shorebirds among land cover types only contained the variable mean shorebird habitat area (Table 2.5, Fig. 2.2). The Akaike weights and sums of the Akaike weights suggest with high certainty that the models only containing area of shorebird habitat were the best models of the abundance and richness of shorebirds at a landscape scale. Migratory shorebird abundance and species richness were positively related to increases in the amount of shorebird habitat regardless of land cover on a landscape scale.

Habitat inundation classes

Next, we examined relationships between each shorebird response group and the area of habitat in each inundation class within landscapes. Candidate model sets included a null model and all additive combinations of habitat inundation classes ($R = 8$). The best approximating models of the abundance and species richness of migratory shorebirds both included the area of permanent and temporary habitat (Table 2.6a). The weights of evidence for these models were high ($w_i = 0.85$ for abundance and 0.68 for richness) and the composite model parameter estimates indicate a positive relationship between the abundance and richness of migratory shorebirds and the amount of these inundation classes at a landscape scale (Table 2.6b). Likewise, the results of the analysis of intermediate and long distance migrants included area of permanent and temporary habitats. All of the top models of intermediate and long distant migrant abundance and species richness were well supported, and the composite parameters indicate positive trends.

Contrastingly, the most parsimonious models for the resident group only included the landscape area of habitat in the permanent inundation class (Table 2.6a). Increases in the area of permanent habitat were positively related to both the abundance and species richness of resident shorebirds (Table 2.6b). Similarly, models including permanent habitat area were the best approximating models of short distance migrant abundance and richness. However, the models among the "best model" candidate set also included single variable models with the predictors area of semi-permanent and temporary habitat. For short distance migrant abundance, the model including permanent habitat had 2.5 times more support over the next top model, while for short distance species richness, the model had 4.2 times the support (Table 2.6a). However, the summed Akaike weights indicate that permanent and temporary habitat are both important predictors of the short distance migrant abundance ($w_+(j)$ = 0.45, 0.26, respectively) and species richness ($w_+(j)$ = 0.39, 0.36, respectively), but semi-permanent habitat was also plausible ($w_+(j)$ =0.05, 0.12 respectively). All of the composite model parameters indicate that positive increases in these habitat inundation classes increase the abundance and species richness of short distance migrant shorebirds within landscapes (Table 2.6b).

Within habitat inundation classes

The focus of this analysis was to examine relationships between the abundance and species richness of each shorebird group and the total area of habitat in each wetland category within each inundation class. Candidate model sets included a null model and all additive combinations of wetland categories within permanent, semi-permanent and temporary inundation classes (R = 8, 8 and 4, respectively). Within inundation classes, migratory shorebird abundance was best supported by models that contained the predictors area of permanent riverine and lacustrine habitat, area of semi-permanent floodwater and palustrine habitat, and area of temporary floodwater habitat (Table 2.7). Only the top models from the analysis between migratory shorebird abundance and semi-permanent habitats had similar Akaike weights (w_i =

0.37 and 0.31, respectively). The top models selected from the analysis of migrant species richness within inundation classes were generally similar to those selected for abundance. Although, within permanent habitats the model selected only contained the variable permanent riverine habitat and the palustrine habitat model was also well supported within the temporary class.

The analysis and model selection procedure yielded consistent results between resident shorebird abundance and species richness within each inundation class (Table 2.7). The model sets selected in the permanent class both included three single variable models with each permanent wetland category. The model with the variable area of lacustrine habitat was the top model selected for resident species abundance and species richness. In the case of resident species richness, this model was 2.2 times more plausible than the riverine habitat model. However, for resident species abundance, all three permanent wetland categories had almost equal support given the data and candidate model set. One model was selected for both abundance and richness in the semi-permanent and temporary classes. The models included the variables semi-permanent palustrine and floodwater and temporary palustrine. The AIC_c weights of the top models in the semi-permanent and temporary classes indicate that these models were all well supported.

Among the shorebird groups based on migration distance, the top models selected for short distant migrant abundance and species richness within permanent habitats only included the variable area of lacustrine habitat (Table 2.7). This was in contrast to the top models for both intermediate and long distance migrant abundance and richness that contained area of riverine habitat. The model selection results within the semi-permanent inundation class consistently indicted that floodwater habitat was a highly supported explanation of the abundance and species richness of each of these shorebird groups. For intermediate and long distance migrant shorebird abundance and species richness, the best supported models within temporary habitat all included

floodwater habitat. However, for short distance migrant abundance and species richness, the null model was selected from the candidate set of temporary habitats.

Among all habitat types

Next, we examined relationships between the abundance and species richness of each shorebird group and the total area of habitat in each wetland category among inundation classes. Hence, unlike the previous analysis, we did not restrict our examinations to the relative influence of each wetland category within each inundation class on a response group. Rather, for each shorebird response group, we collectively examined the relative influence of all of the shorebird habitat types. For each analysis and selection procedure, we constructed and compared a null model and all possible additive combinations of each global model ($R = 256$).

The best approximating model of migratory shorebird abundance included the variables area of permanent lacustrine and riverine habitat and temporary floodwater habitat (Table 2.8a). The sums of the Akaike weights indicate that all variables in the "best model" set were important predictors of migratory shorebird abundance (Table 2.8b). The " best model" set for the response migratory shorebird species richness was the same except it included semi-permanent floodwater habitat instead of lacustrine habitat (Fig. 2.3). The abundance and richness of migratory shorebirds were positively related to increases in all of the variables (Table 2.8b).

For the response group resident shorebirds, only habitats within the permanent and semi-permanent inundation classes were positively related to abundance and species richness. The difference in AIC_c values among the selected models for resident abundance and species richness indicate support for multiple models (Table 2.8a). The sums of the Akaike weights suggest that the area of permanent lacustrine and semi-permanent palustrine habitats were important predictors of resident abundance and species richness. However, the area of permanent riverine habitat was only an important predictor of species richness and the area of semi-permanent floodwater habitat was only an important predictor of abundance (Table 2.8b).

Contrasting results existed among the habitat types included in the "best model" sets for the shorebird groups based on migration distance (Table 2.8a). The model sets selected to explain the abundance and species richness of short distance migrants both included one model. Both models included the variable area of permanent lacustrine habitat, but semi-permanent floodwater habitat was also an important predictor of species richness ($w_+(j) = 0.93$, Table 2.8b). The top model of species richness of intermediate distance migrants included permanent riverine and semi-permanent floodwater habitat and was well supported given the data and candidate model set (Table 2.8a). The "best model" set for intermediate distance migrant abundance included permanent riverine, semi-permanent floodwater, and temporary floodwater and temporary palustrine habitat types. However, the sums of the Akaike weights indicate that permanent riverine and floodwater habitats were the most important predictors of intermediate distance migrant abundance and species richness (Table 2.8b). Temporary floodwater habitat was the most important predictor of the abundance and richness of long distance shorebird migrants ($w_+(j) = 0.94, 0.99$, respectively). Composite parameter results indicate that all trends between groups and habitat area were positive.

DISCUSSION

Our results show that the landscape area of shorebird habitat influences the abundance and diversity of migratory shorebirds within landscapes regardless of the area of other semi-natural and developed land cover types surrounding the habitat. Furthermore, the response of shorebirds to the landscape composition of different habitat types varied with migration distance and breeding status. True landscape-level studies in which landscapes are used as replicates are extremely rare in the literature (Thorton et al. 2011) and we are unaware of any studies that have examined landscape influences on migrating shorebirds. Our findings provide empirical evidence that the habitat composition of entire landscapes, not just individual habitat patches, should be

examined for wide ranging migratory shorebirds, especially when considering conservation strategies for these imperiled species.

The abundance and species richness of migratory shorebirds linearly increased with the area of shorebird habitat within landscapes similar to patterns reported in other studies (Buler et al. 2007). The theoretical model generally used to understand the process of habitat selection used by migratory birds implies that birds initially select among en route stopover areas based on broad-scale characteristics and proceed to finer-scale habitat features within stopovers (Hutto 1985; Moore and Aborn 2000; Deppe and Rotenberry 2008). En route migratory birds use landscape-level habitat composition as a coarse-level cue to select a landing site at the end of a migratory flight and subsequently, this choice may determine the distribution of migrants within a region (Buler et al. 2007). We further suggest that by selecting landscapes with greater amounts of stopover habitat, migrating shorebirds are more likely to minimize the energetic costs associated with locating resources, with improved energetic intake because more habitat is available within shorter distances (Farmer and Parent 1997). Positive relationships between migratory shorebird richness and the area of wetland habitat within landscapes is not surprising considering that species richness generally increases with habitat area because more habitats are available to accommodate more interspecific niche requirements (MacArthur and Wilson 1967).

We found no evidence that the area of developed or semi-natural land cover affected the abundance and richness of migratory shorebirds among landscapes. Direct comparisons with other studies are limited because landscape-level studies mainly examine the influence of landscape context variables (e.g., habitat composition or configuration measured from a focal habitat patch using buffers, linear distance measured between patches, or connectivity metrics) on the habitat-use patterns of migrating birds or treat non-habitat within landscapes as a neutral matrix (Thorton et al. 2011). Skagen et al. (2005) examined the relationship between the amount of different habitat types and occurrence of migratory shorebird species and found a positive

relationship between the amount of cropland and the occurrence of several migratory shorebird species, but they found no relationship with grassland area. Comparably, Webb et al. (2010a) found no relationship between the abundance of migratory shorebirds within focal wetlands and the area of grassland or cropland land cover within a 10 km buffer. However, we contend that while factors related to the types of land cover surrounding a wetland may influence the use of a wetland, coarse-level selection initially based on the landscape composition of habitat may allow individual birds to rapidly assess potential habitat quality. Once birds settle into a landscape with abundant habitat, they can refine their distributions based on finer scale attributes and have a greater likelihood of encountering at least some suitable habitat patches. Thus, the potential benefits of abundant wetland habitat within a landscape may consistently supersede any negative aspects associated with the matrix in which habitat patches are nested. The rapid assessment of potential habitat quality may be an important aspect of habitat selection particularly when we consider the ecological and physiological challenges associated with migration (Moore et al. 1995, 2005). This may be especially true for interior migrating shorebirds because they encounter wide spatio-temporal variation in the distribution of wetland resources (Skagen and Knopf 1993; Skagen et al. 2008; Albanese 2011).

Our results indicate that the landscape area of permanent lacustrine habitat was an important predictor of migratory shorebird abundance, but not of species richness. However, permanent riverine and more transitory floodwater habitats were important predictors of both species richness and abundance. Landscapes with abundant permanent lacustrine habitat accommodate large concentrations of shorebirds, but the small number of microhabitats associated with this type of habitat may limit the number of species. During migration, the use of wetland habitat varies among shorebird species as vegetation cover, water depth, and ratio of saturated substrate and shallow water changes (Skagen and Knopf 1994; Davis and Smith 1998, 2001), and increased variation in these factors is positively related with the occurrence and

abundance of migrating shorebirds within wetlands (Niemuth et al 2006; Webb et al. 2010a). Additionally, wetland structural complexity facilitates a greater diversity of macroinvertebrates within wetlands (Olsen et al. 1995; Kostecke et al. 2005), greater prey accessibility (Colwell 2010) and allows multiple shorebird species with different niche requirements to co-occur (Webb et al. 2010b). Within our study area, the shoreline of lacustrine wetlands were generally homogenous in water depth, vegetation cover, and ratio of saturated substrate to water, while riverine and floodwater wetlands typically encompassed a broader range of variation among these same factors. When large areas of riverine or floodwater habitats were present in a landscape, a wider suite of microhabitats were available, and thus, landscapes were capable of accommodating both higher numbers of shorebirds and a greater diversity of species.

In our study area, riverine and lacustrine wetlands were typically distinct and dominant landscape features. In contrast, landscapes with abundant temporary floodwater habitat were comprised of many relatively small and discrete habitat patches that individually hosted relatively low numbers of shorebirds and species, but collectively provided habitat for high numbers of individuals and species. Several studies have highlighted the importance of ephemeral wetlands to shorebirds migrating through midcontinental North America (Davis and Smith 1998; Niemuth et al. 2006; Skagen et al. 2008), but unlike previous research, our study focused on the comparative importance of wetland types to shorebirds at a landscape-level. Most notably, Skagen et al. (2008) demonstrated the importance of ephemeral wetlands in the Northern Great Plains of North America to migrating shorebirds. They argued that because of their smaller size, lack of large and discrete shorebird congregations, and their shifting and unpredictable nature in time and space, the vital role that these wetlands play in providing stopover resources has been traditionally overlooked. Our results further emphasize the importance of these habitats because they indicate that beyond providing vital stopover resources at fine scales, landscapes with

abundant ephemeral wetland habitats are important component of numerous and diverse migratory shorebird assemblages.

The landscape-level importance of ephemeral wetlands presents a potential challenge to shorebird conservation efforts when we consider forecasts of further depletion of these wetlands in the face of predicted agricultural intensification and climate change within the region (Poiani and Johnson 1991; Tilman 2001; Johnson et al. 2010). Several lines of research have shown that habitat fragmentation beyond certain thresholds can alter the habitat-use patterns of birds within landscapes (Andŕen 1994). Similarly, our results indicate that reductions in the amount of habitat that comprise landscape-level wetland complexes negatively influenced migratory shorebird abundance and richness in landscapes. Additionally, in a related study, Albanese (2011) showed that patch level habitat-use patterns of migrating shorebirds were best explained by wetland habitat density at broad spatial scales and the occurrence of shorebirds within habitats increased with broad-scale habitat density. Furthermore, they elucidated relationships between local weather patterns and the spatiotemporal distribution of shorebird wetland habitat. Within this dynamic system, sporadic local, heavy precipitation events created landscapes with abundant temporary wetland habitats, while during extended dry conditions, habitat was absent or limited to wetlands that were more permanent. We suggest that the presence of abundant ephemeral habitats may play a vital role in the higher-level phases of the hierarchal process of habitat selection by facilitating the selection of habitat at broad spatial scales. The depletion of these wetlands among landscapes may not only eliminate patch-level use of ephemeral wetlands, but also preclude the use of other more permanent wetlands types within landscapes because of the collective capacity of these wetlands to produce landscape-level wetland complexes with abundant habitat.

When we compared the models selected that best explained the abundance and species richness of different shorebird groups, several interesting patterns emerged. The models selected

for resident species abundance and richness solely included habitat in the permanent and semi-permanent inundation classes. However, the amount of area occupied by both permanent and temporary wetland habitats were important predictors of migratory species richness and abundance. To meet the requirements associated with the breeding portion of their life cycle, shorebird species breeding in the region likely require the longer hydroperiods of more permanent wetland types (Conway et al. 2005a, 2005b). However, this constraint does not apply to migratory shorebirds that forage and use habitat opportunistically during migration (Skagen and Knopf 1994; Skagen and Oman 1996; Davis and Smith 2001). In order to successfully complete the next leg of migration, the wetland resources required by a shorebird need only be accessible over a relatively short residency period (i.e., hours to days), and decisions by a bird to continue migration or remain at a stopover site may be based on the bird's present condition and the quality and availability of wetland habitats along the entire route (Colwell 2010).

Among all habitat types, the landscape area of floodwater habitats was an important predictor of the abundance and species richness of both intermediate and long distance migrants. The occurrence of abundant floodwater habitat is especially variable and unpredictable within the interior of North America (Albanese 2011). This further emphasizes that the migratory movements of shorebirds are characterized by broad dispersion and opportunism throughout the region (Skagen and Knopf 1993; Skagen et al. 2008). Broad-scale expanses of high-density floodwater habitat occurred after heavy precipitation, and the resulting habitats within the flooded wetland complexes provided highly connected habitats at the broad spatial scales that best explained migrant shorebird distribution patterns (Albanese 2011). When abundant in a landscape, floodwater habitats were generally characterized by substantial mud flats and shallow water within the range of shorebird foraging depths (i.e., < 16 cm) (Davis and Smith 1998). When replete, these transient habitats expose previously inaccessible and plausibly abundant prey resources to foraging shorebirds. Migrating shorebirds can process food and assimilate energy at

exceedingly high rates (Kvist and Lindstrom 2003) and fat reserves increase with impending migration distance (Piersma and Gill 1998). The broad and fine-scale characteristics of abundant floodwater habitat may best provide efficient and gainful access to the food resources necessary to successfully complete migration under the severe physiological demands and temporal constraints of long distance travel. Contrastingly, we suggest that the lack of evidence we found for the importance of temporary habitats to short distance migrants may reflect the less rigorous time constraints and physiological demands of a shorter migration route and more southerly breeding distribution. These species may better afford the additional time and energy that may be necessary to locate resources at broad and fine spatial scales in more predictable and stable habitats.

This landscape-level examination is the first study that we are aware to elucidate the broad-scale habitat-use patterns of these declining birds. We conclude that true landscape-scale studies can provide important additional insights on the influence of broad-scale factors on en route migratory birds. Our results provide needed information on current use patterns and the importance of different types of migration stopover wetlands to shorebirds within the Great Plains of North America. For widely dispersed migratory shorebird populations traveling through this region, broad-scale wetland complexes with abundant shorebird habitat support plentiful and rich shorebird communities. Shorebird habitat associated with riverine and ephemeral wetlands may be especially important to species that migrate longer distances to and from wintering and breeding grounds. These findings combined with a lack of comprehensive legal protection and forecasts of pervasive land use change further emphasize the need for conservation efforts directed at wetland landscapes. As long as these wetland habitats are imperiled, conservation organizations will need to prioritize landscapes according to their potential to provide abundant wetland habitat at the broad scales necessary to accommodate these wide-ranging populations. For midcontinental migrant shorebirds, we recommend that efforts be focused on landscape-level

wetland complexes that include a mixture of abundant permanent riverine habitats with a large compliment of potential ephemeral floodwater habitats. This will best accommodate both abundant and rich species assemblages within these continually changing landscapes.

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Table 2.1. Composition of land cover classes and subclasses present among ten landscapes in north-central Oklahoma, US. Wetland shorebird habitat was defined as areas that potentially contain saturated substrate and shallow water (<16 cm) within wetlands and around wetland edges.

Land cover type	Mean (ha)	SE	Minimum	Maximum
Total Developed	16079.4	2293.0	6669.3	25863.1
Urban/suburban	3952.8	2180.1	1021.0	23483.5
Row cropland	12052.0	2222.0	2287.1	21141.5
Total Semi natural	13294.4	2146.6	3030.1	22994.8
Barren	281.2	269.7	3.1	2708.1
Forest/shrubland	1657.5	569.0	31.4	5592.1
Grassland/pasture	11430.2	1827.1	2302.6	22373.8
Wetland	869.0	511.8	34.6	5180.5
Total potential shorebird habitat	1173.3	430.1	140.4	4885.4

Table 2.2. List of shorebird species encountered within wetland habitats in north-central Oklahoma, US, 2007-2009. Group assignments used for analysis are also listed and were based on current breeding status and the migration distance.

Species	Group assignment [a]				
	M	R	S	I	L
Black-bellied Plover *(Pluvialis squatarola)*	X			X	
American Golden-Plover *(Pluvialis dominica)*	X				X
Snowy Plover *(Charadrius alexandrinus)*		X			
Semipalmated Plover *(Charadrius semipalmatus)*	X			X	
Killdeer *(Charadrius vociferus)*		X			
American Avocet *(Recurvirostra americana)*[b]	X		X		
Black-necked Stilt *(Himantopus mexicanus)*[b]	X		X		
Willet *(Tringa semipalmata)*	X		X		
Lesser Yellowlegs *(Tringa flavipes)*	X			X	
Greater Yellowlegs *(Tringa melanoleuca)*	X			X	
Solitary Sandpiper *(Tringa solitaria)*	X			X	
Spotted Sandpiper *(Actitis macularius)*		X			
Whimbrel *(Numenius phaeopus)*	X			X	
Long-billed Curlew *(Numenius americanus)*	X		X		
Hudsonian Godwit *(Limosa haemastica)*	X				X
Marbled Godwit *(Limosa fedoa)*	X		X		
Ruddy Turnstone *(Arenaria interpres)*	X			X	
Red Knot *(Calidris canutus)*	X			X	
Sanderling *(Calidris alba)*	X			X	
Dunlin *(Calidris alpina)*	X			X	
Semipalmated Sandpiper *(Calidris pusilla)*	X			X	
Western Sandpiper *(Calidris mauri)*	X			X	
Least Sandpiper *(Calidris minutilla)*	X			X	
White-rumped Sandpiper *(Calidris fucicollis)*	X				X
Pectoral Sandpiper *(Calidris melanotos)*	X				X
Baird's Sandpiper *(Calidris bairdii)*	X				X
Buff-breasted Sandpiper *(Tryngites subruficollis)*	X				X
Long-billed Dowitcher *(Limnodromus scolopaceus)*	X			X	
Wilson Snipe *(Gallinago delicate)*	X		X		
Stilt Sandpiper *(Calidris himantopus)*	X				X
Wilson's Phalarope *(Phalaropus tricolor)*	X			X	
Red-necked Phalarope *(Phalaropus lobatus)*	X			X	

[a] M = migrant/non breeder, R = resident/common breeder (Reinking 2004), S = short distant migrant, I = intermediate distant migrant, L = long distant migrant (Skagen and Knopf 1993).

[b] Species rarely breed in most of study area.

Table 2.3. Summary statistics of shorebird wetland habitat present during the study among ten landscapes in north-central Oklahoma, US, 2007-2009. Statistics include the total sample of habitat patches surveyed in each inundation class and wetland category, the mean and SE of the estimates of the habitat area present, and the mean proportion (prop.) and SD of the number of surveyed habitat patches with habitat present during a survey.

Habitat Class Habitat Category	n	Mean (ha)	SE	Mean prop.	SD
Permanent	3652	322.3	34.9	0.67	0.47
Lacustrine	582	56.6	11.7	0.47	0.50
Riverine	1287	216.0	24.1	0.76	0.43
Palustrine	1783	49.7	2.4	0.68	0.47
Semi-permanent	4211	181.3	22.2	0.64	0.48
Floodwater	446	34.0	3.6	0.79	0.41
Palustrine	2631	62.3	3.1	0.76	0.43
Wastewater impoundment	393	3.7	0.5	0.26	0.44
Temporary	6581	172.4	14.6	0.48	0.50
Floodwater	5958	161.3	14.3	0.69	0.46
Palustrine	623	11.1	1.0	0.46	0.50

Table 2.4. Summary of the abundance and species richness of shorebirds surveyed in ten landscapes in north-central Oklahoma, US, 2007-2009.

Shorebird group	Mean	SE
Shorebird abundance		
Total migrants per landscape	3840.8	2883.2
Total migrants per interval	158.4	31.4
Total residents per interval	37.5	4.3
Total short distance migrants per interval	9.9	2.7
Total intermediate distance migrants per interval	91.9	18.0
Total long distance migrants per interval	54.8	14.5
Species richness		
Total migratory species per landscape	13.6	2.5
Total migratory species per interval	3.9	0.4
Total resident species per interval	1.7	0.1
Total short distance migrant species per interval	0.6	0.1
Total medium distance migrant species per interval	2.4	0.2
Total long distance migrant species per interval	0.9	0.1

Table 2.5. (A) Minimum ΔAIC_c ($\Delta AICc < 6$ [a]) and Akaike weights of multi linear regression models of migratory shorebird abundance and species richness dependent on total shorebird habitat area, total semi-natural land cover area and total developed land cover area within landscapes. (B) Composite model parameter estimates and summed Akaike weights of explanatory variables in selected models.

(A) Summary of selected alternative models:

Response group	Model	ΔAIC_c	Akaike weight
Abundance	Mean shorebird habitat area	0	0.63
Richness	Mean shorebird habitat area	0	0.46

(B) Summary of composite parameters for variables in best supported models:

	Abundance		Richness	
Parameter	Model averaged coefficients	Summed Akaike weights	Model averaged coefficients	Summed Akaike weights
Mean shorebird habitat area	364.75	0.99	4.42	0.97

[a] Alternative candidate models were only selected for the "best model" sets when the AICc value for a model was less than the AICc values of all the simpler models within which they were nested (Richards 2008).

Table 2.6. (A) Minimum ΔAIC_c ($\Delta AICc < 6$ [a]) and Akaike weights of time-series regression models of abundance and richness of shorebird response groups dependent on total area of wetland shorebird habitat in each inundation class within landscapes. (B) Composite model parameter estimates and summed Akaike weights of explanatory variables in selected models.

(A) Summary of selected alternative models:

Response group	Selected alternative models	ΔAIC_c	Akaike weight
All migrants			
Abundance	Permanent, temporary	0	0.85
Richness	Permanent, temporary	0	0.68
Resident			
Abundance	Permanent	0	0.80
Richness	Permanent	0	0.81
	Semi-permanent	4.91	0.07
Short distance			
Abundance	Permanent	0	0.32
	Temporary	1.78	0.13
	Semi-permanent	5.35	0.02
Richness	Permanent	0	0.30
	Temporary	2.84	0.07
	Semi-permanent	4.54	0.03
Intermediate distance			
Abundance	Permanent, temporary	0	0.89
Richness	Permanent, temporary	0	0.88
Long distance			
Abundance	Permanent, temporary	0	0.67
	Permanent	3.59	0.11
Richness	Permanent, temporary	0	0.90

(B) Summary composite parameters of variables in best supported models:

	Abundance		Richness	
Parameter	Model averaged coefficients	Summed Akaike weights	Model averaged coefficients	Summed Akaike weights
All migrants				
Permanent	40.93	1.0	3.74	1.0
Temporary	3.13	1.0	1.95	1.0

Table 2.6. cont.

(B) Summary composite parameters of variables in best supported models:

Parameter	Abundance		Richness	
	Model averaged coefficients	Summed Akaike weights	Model averaged coefficients	Summed Akaike weights
Resident				
Permanent	3.21	0.99	1.43	0.90
Semi-permanent	NA	NA	1.35	0.13
Short distance				
Permanent	1.93	0.45	1.65	0.39
Semi-permanent	1.03	0.05	1.08	0.12
Temporary	1.40	0.26	1.23	0.36
Intermediate distance				
Permanent	27.47	1	4.56	0.99
Temporary	2.92	1	1.70	0.98
Long distance				
Permanent	7.21	0.94	2.98	1
Temporary	4.60	0.84	1.76	1

[a] Alternative candidate models were only selected for the "best model" sets when the AICc value for a model was less than the AICc values of all the simpler models within which they were nested (Richards 2008).

Table 2.7. Minimum ΔAIC_c ($\Delta AICc < 6$ [a]) and Akaike weights of time-series regression models of abundance and richness of shorebird response groups dependent on the total area of each wetland category in each inundation class within landscapes.

Response group	Selected alternative models	ΔAIC_c	Akaike weight
	Permanent inundation class		
All migrants			
Abundance	Riverine, lacustrine	0	0.41
Richness	Riverine	0	0.71
Resident			
Abundance	Lacustrine	0	0.22
	Riverine	0.02	0.21
	Palustrine	1.69	0.18
Richness	Lacustrine	0	0.29
	Riverine	1.56	0.13
	Palustrine	4.91	0.05
Short distance			
Abundance	Lacustrine	0	0.45
Richness	Lacustrine	0	0.47
	Palustrine	4.67	0.04
Intermediate distance			
Abundance	Riverine	0	0.53
Richness	Riverine	0	0.82
Long distance			
Abundance	Riverine	0	0.61
Richness	Riverine	0	0.76
	Semi-permanent inundation class		
All migrants			
Abundance	Floodwater, palustrine	0	0.37
	Floodwater	0.38	0.31
Richness	Floodwater	0	0.75
Resident			
Abundance	Floodwater, Palustrine	0	0.70
Richness	Floodwater, Palustrine	0	0.72
Short distance			
Abundance	Floodwater	0	0.47
Richness	Floodwater	0	0.63
	Palustrine	2.50	0.18

Table 2.7. cont.

Response group	Selected alternative models	ΔAIC_c	Akaike weight
	Semi-permanent inundation class		
Intermediate distance			
Abundance	Floodwater, palustrine	0	0.45
	Floodwater	1.36	0.23
Richness	Floodwater, palustrine	0	0.51
	Floodwater	0.26	0.45
Long distance			
Abundance	Floodwater	0	0.60
Richness	Floodwater	0	0.75
	Temporary inundation class		
All migrants			
Abundance	Floodwater	0	0.54
Richness	Floodwater	0	0.56
	Palustrine	1.91	0.22
Resident			
Abundance	Palustrine	0	0.69
Richness	Palustrine	0	0.47
Short distance			
Abundance	NA [b]	NA	NA
Richness	NA	NA	NA
Intermediate distance			
Abundance	Floodwater	0	0.61
	Palustrine	2.48	0.18
Richness	Floodwater	0	0.44
	Palustrine	0.69	0.31
Long distance			
Abundance	Floodwater	0	0.91
Richness	Floodwater	0	0.96

[a] Alternative candidate models were only selected for the "best model" sets when the AICc value for a model was less than the AICc values of all the simpler models within which they were nested (Richards 2008).

[b] Model or value not included because the null model had the lowest AIC_c value among the alternative models in the candidate model set.

Table 2.8. (A) Minimum ΔAIC_c ($\Delta AICc < 6$ [a]) and Akaike weights of best supported time-series regression models for abundance and richness of shorebird response groups dependent on total area of wetland shorebird habitat among all wetland inundation classes and wetland categories within landscapes. (B) Composite model parameter estimates and summed Akaike weights of explanatory variables in selected models.

(A) Summary of selected alternative models:

Response group	Selected alternative models	ΔAIC_c	Akaike weight
All migrants			
Abundance	Perm. lacustrine, perm. riverine, temp. floodwater	0	0.46
	Perm. lacustrine, temp. floodwater	1.55	0.21
	Perm. lacustrine, perm. riverine	4.27	0.06
Richness	Perm. riverine, temp. floodwater, semi floodwater	0	0.41
	Temp. floodwater	2.52	0.11
Resident			
Abundance	Semi. floodwater	0	0.67
	Perm. lacustrine, semi. palustrine	2.07	0.24
	Perm. palustrine, semi. palustrine	5.59	0.04
Richness	Perm. lacustrine	0	0.38
	Semi. palustrine	0.28	0.33
	Perm. riverine	1.57	0.17
	Perm. palustrine	4.92	0.03
Short distance			
Abundance	Perm. lacustrine	0	0.39
Richness	Perm. lacustrine, semi. floodwater	0	0.26
Intermediate distance			
Abundance	Perm. riverine, semi. floodwater, temp. floodwater	0	0.33
	Perm. riverine, temp. floodwater	0.29	0.29
	Perm. riverine, temp. palustrine	3.00	0.07
	Semi. floodwater, temp. floodwater	4.09	0.04
	Temp. floodwater	4.45	0.04
	Perm. riverine, semi. floodwater	5.29	0.02
Richness	Perm. riverine, semi. floodwater	0	0.42
	Perm. riverine, temp. floodwater	4.34	0.05
Long distance			
Abundance	Semi. floodwater, temp. floodwater	0	0.33

Table 2.8. cont.

(A) Summary of selected alternative models:

Response group	Selected alternative models	ΔAIC_c	Akaike weight
Long distance			
Abundance	Temp. floodwater	0.27	0.32
	Semi. floodwater	3.80	0.05
Richness	Temp. floodwater	0	0.53

(B) Summary composite parameters of variables in best supported models:

	Abundance		Richness	
Parameter	Model averaged coefficients	Summed Akaike weights	Model averaged coefficients	Summed Akaike weights
All migrants				
Perm. lacustrine	2.10	0.89	NA	NA
Perm. riverine	1.81	0.68	1.44	0.70
Semi. floodwater	NA	NA	1.36	0.32
Temp. floodwater	2.30	0.95	2.03	0.99
Resident				
Perm. lacustrine	1.07	0.25	1.10	0.43
Perm. riverine	NA	NA	1.09	0.21
Perm. palustrine	1.10	0.08	1.03	0.06
Semi. floodwater	1.24	0.71	NA	NA
Semi. palustrine	1.28	0.29	1.34	0.38
Short distance				
Perm. lacustrine	1.42	0.75	1.28	0.58
Semi. floodwater	NA	NA	1.31	0.48
Intermediate distance				
Perm. riverine	2.19	0.88	1.50	0.95
Semi. floodwater	1.87	0.50	1.56	0.93
Temp. floodwater	2.19	0.82	1.40	0.48
Temp. palustrine	1.67	0.25	NA	NA
Long distance				
Semi. floodwater	1.27	0.50	NA	NA
Temp. floodwater	2.31	0.94	1.71	0.99

[a] Alternative candidate models were only selected for the "best model" sets when the AICc value for a model was less than the AICc values of all the simpler models within which they were nested (Richards 2008).

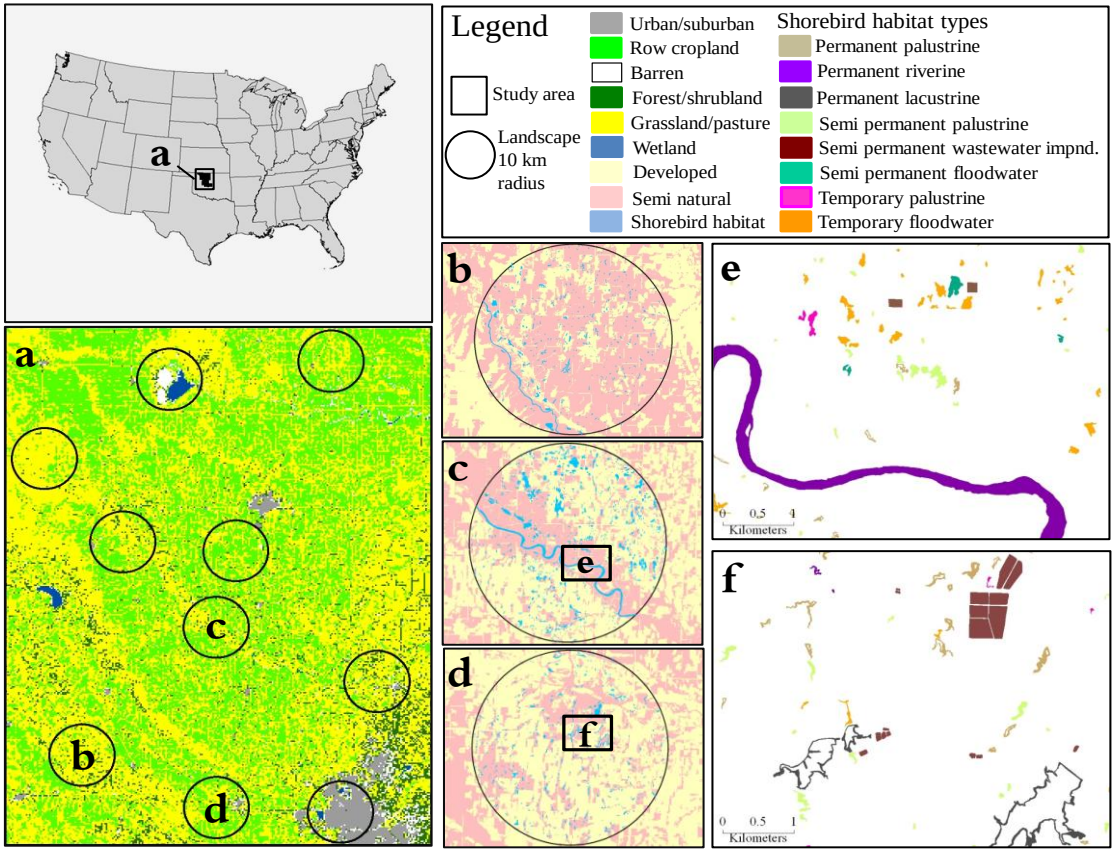
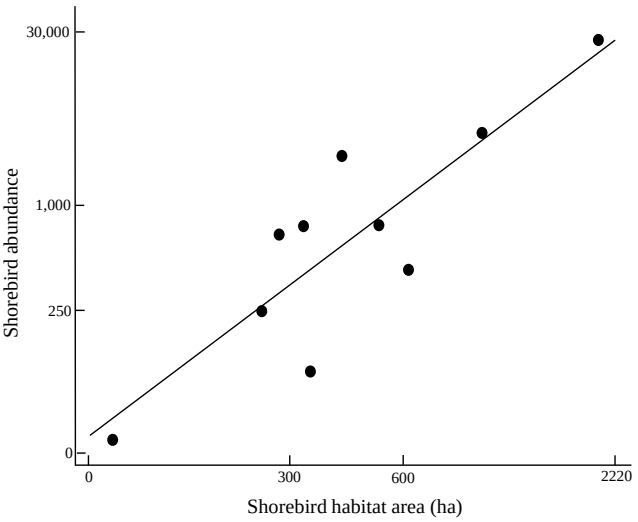


Figure 2.1. Study area and landscapes in north-central Oklahoma, US. The location of the ten study landscapes and the distribution of initial land cover types is shown (image a). The distribution of the condensed land cover and potential wetland shorebird habitat classes used in the analysis are shown for three of the landscapes in images b thru d. Examples of the distribution of wetland shorebird habitat inundation classes and categories within landscapes are shown in images e and f.



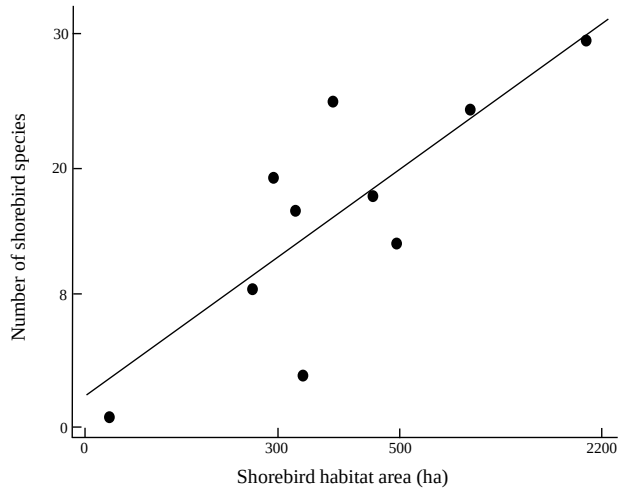


Figure 2.2. Relationship between abundance and species richness of migratory shorebirds and the mean area of wetland shorebird habitat within a landscape. (a) Relationship between the number of migratory shorebirds and the mean area of wetland shorebird habitat within landscapes: log (y) = -3.803 + 2.459 x log(x); r^2 = 0.73, n = 10. (b) Relationship between the number of migratory shorebird species and the mean area of wetland shorebird habitat within landscapes: log (y) = 0.5297 + 0.6038 x log(x); r^2 = 0.59, n = 10. Note graph axis values are untransformed.

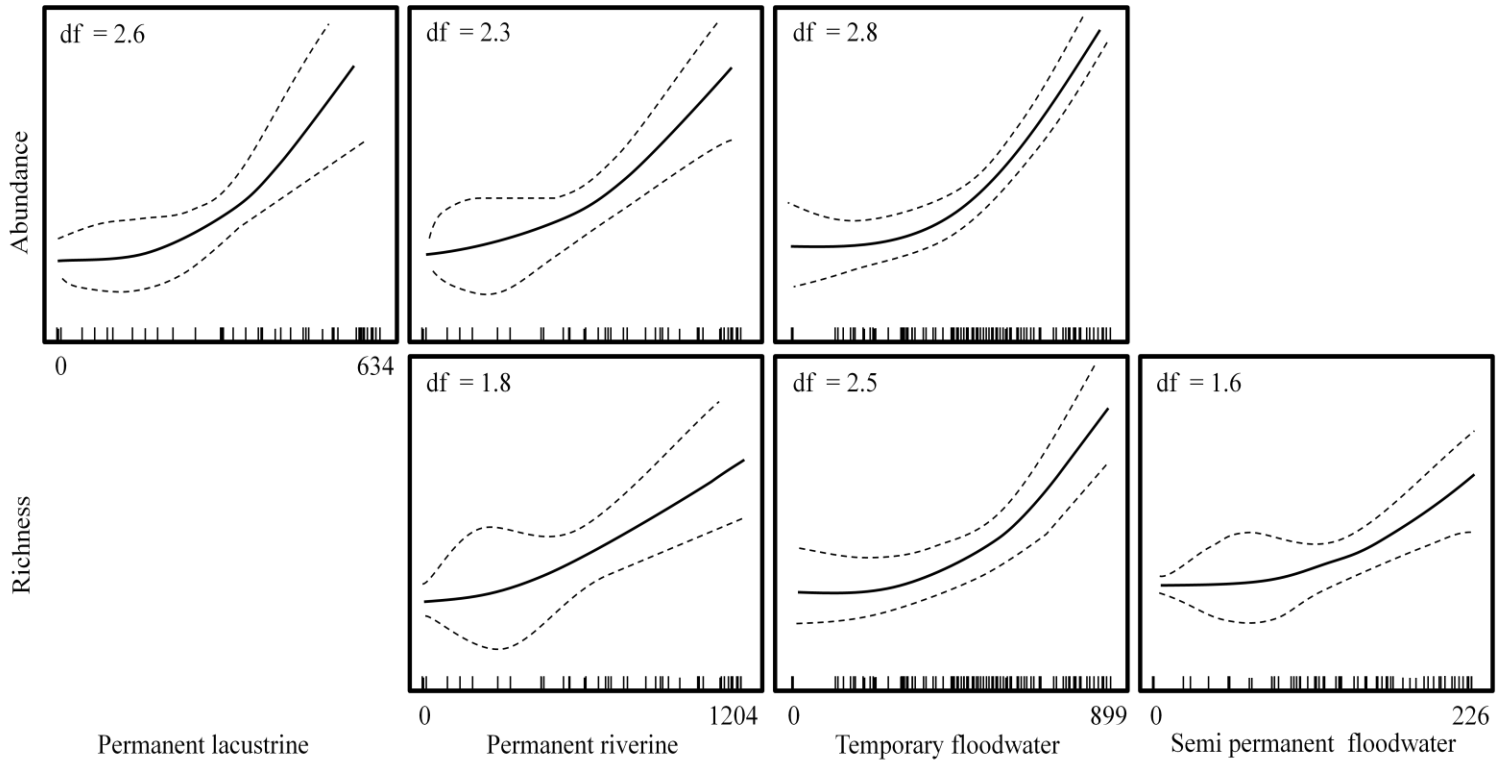


Figure 2.3. Estimated smoothing curves contrasting the best approximating model of migratory shorebird abundance (top row) and species richness (bottom row). The explanatory variables in each model are listed at the bottom of each column. Each curve was estimated holding all other explanatory variables in the model constant. The estimated degrees of freedom contributed by each smoother to the fitted values are listed within each graph. The solid line is the smoother and the dotted lines are the 95% confidence bands. The small vertical lines along the x-axis indicate the location of habitat area values of each observation. Values on the x-axis are hectares and untransformed.

CHAPTER III

A COMPARATIVE EXAMINATION OF WITHIN WETLAND AND WETLAND CONTEXT CHARACTERISTICS ON STOPOVER HABITAT USE BY MIGRATORY SHOREBIRDS: IS THE NEIGHBORHOOD IMPORTANT?

ABSTRACT

Wetland stopover use by migratory shorebirds is concurrently influenced by habitat characteristics present within a stopover and characteristics related to the broader context surrounding the stopover. In order to conserve the stopover habitats essential for shorebirds to complete migration through the interior of North America, it is necessary to have an understanding how these factors influence stopover use. We conducted surveys of wetland stopover habitats within ten broad-scale landscapes in north-central Oklahoma from 2007 thru 2009 to determine how intra habitat and habitat context characteristics influence the abundance of migrating shorebirds within wetland stopovers. We used zero-inflated modeling and an information theoretic framework to separately examine and then compare the relative importance of intra habitat variables and habitat context variables in explaining the differential use of wetland stopovers. Among intra habitat variables, we found that shorebirds stopover in greater abundance in large wetland habitats that were sparsely vegetated with shallow slopes. Among habitat context variables, shorebird abundance increased with shorebird habitat density at a 2 km scale and grazing intensity. Land cover context was also important in explaining shorebird abundance. When compared to the models with intra habitat variables, models containing habitat context

variables better explained migratory shorebird abundance. We conclude that characteristics related to the broader context surrounding a wetland stopover strongly influence stopover use by migratory shorebirds. Conservation and management of migratory shorebirds should aim to provide large, sparsely vegetated and shallow sided wetland stopover habitats in an open land context within areas of high-density shorebird habitat.

Key words: Avian migration, habitat use, landscape context, prairie wetlands, shorebird, zero-inflated models.

INTRODUCTION

Understanding the factors that influence migrant shorebird use of wetland stopover sites in the central Great Plains has important conservation implications for this imperiled group of birds (Skagen and Knopf 1993; Skagen 2006). For shorebird species reliant on wetland resources, large-scale land use change and loss of wetlands (Brown et al. 2005; Dahl and Allord 1996) combined with forecasts of further wetland loss and degradation (Johnson et al. 2010) and projections for a changing climate (IPCC 2007) and more intensive agricultural practices (Tilman et al. 2001) have raised serious questions about the ability of these birds to maintain current migration patterns and concerns of imminent population declines (Skagen 2006). Given the considerable physiological and ecological challenges that birds encounter during migration (Moore et al. 1995, 2005), predictions of further unprecedented changes to the contemporary landscape of the central Great Plains highlight the urgency to reliably understand the current stopover-use patterns of migrant shorebirds. This information may prove critical to developing effective conservation strategies for these migratory birds.

Generally, shorebirds associated with wetland habitats during migration select wetland areas that are shallow, sparsely vegetated and have considerable mudflat (Colwell 2010). For shorebirds migrating through the central Great Plains, these intra wetland characteristics have

been shown to significantly influence stopover use by shorebirds (Davis and Smith 1998b). Other studies of shorebirds in the region have examined the influence of both intra wetland characteristics and variables related to the land area surrounding wetlands (i.e., patch context variables) (Niemuth et al. 2006; Webb et al. 2010). Although a few studies have found relationships between patch context variables and the distribution patterns of migratory shorebirds, patch context variables typically do not affect the stopover-use patterns of migratory shorebirds as strongly as intra wetland characteristics (Skagen et al. 2005; Niemuth 2006; Webb et al. 2010).

Still, studies that have examined the influence of patch context variables on the stopover-use patterns of migrant shorebirds are few. Whether the presence or abundance of organisms are explained by characteristics at an immediate location or the area surrounding that location poses an interesting ecological question that is a major focus of ecological research (Thorton et al. 2011) with important land management implications for many species (Lindenmayer and Nix 1997; Steffan-Dewenter et al. 2002; Blevins and With 2011). Thus, studies of occurrence and abundance patterns should consider not only the habitat characteristics within a patch but also the broader context surrounding a focal patch because both ultimately influence these patterns (Weins1989). For example, several studies have found that the occurrence and abundance patterns of some bird species during breeding and wintering periods respond more to the characteristics of the surrounding landscape than to local attributes (Pearson 1993; Grand and Cushman 2003; Boscolo and Metzger 2009). Additionally, the abundance and mass gain of migrant birds has been shown to increase with the amount of suitable habitat in the landscape surrounding stopover sites (Buler et al. 2007; Ktitorov et al. 2008). However, although evidence suggests that factors related to patch context may affect habitat use by birds, relatively little information is available on the influence of these factors on the occurrence and particularly abundance patterns of migrant shorebirds within wetland stopovers of the central Great Plains.

The variable and often extreme weather patterns indicative of the midcontinental interior cause the wetlands used by migrant shorebirds for stopover habitat to be dynamic and unpredictable in space and time (Skagen and Knopf 1994; Albanese 2011b). The presence of habitat conditions suitable for shorebird stopover are erratic within wetlands and the distribution of wetland sites that provide suitable stopover habitat are continuously shifting within the landscape. Shorebirds have apparently responded to these patterns by dispersing widely throughout the region during migration and relying on opportunistic habitat use (Skagen and Knopf 1993; Skagen et al. 2008). In order to accommodate for the shifting distributions of wetland habitats and shorebirds within the region, studies of migratory shorebird stopover use need to be conducted over large geographic extents (Skagen et al. 2005) and at scales appropriate to this wide-ranging life history stage (Addicott et al 1987; Wiens 1989). Furthermore, the theoretical model generally used to understand the process of habitat selection used by migratory birds implies that birds initially select among en route stopover areas based on broad-scale characteristics and proceed to finer-scale habitat features within stopovers (Hutto 1985; Moore and Aborn 2000; Deppe and Rotenberry 2008). Empirical evidence suggests that because of the hierarchal nature of stopover habitat selection, initial selection by migrant birds based on the broad-scale composition of potential habitat may preclude the use of some areas with suitable habitat at finer scales (Buler et al. 2007; Albanese 2011b). Collectively, these conditions can result in many zero observations in the data of studies attempting to relate the local abundance distributions of migrant shorebirds to stopover habitat attributes.

Many ecological data sets that measure the abundance or presence of an organism are characterized by many zero observations (Argarwal et al. 2002; Martin et al. 2005). Data sets with a high proportion of zero values are referred to as zero inflated because they contain more zero values than would be expected for distributions traditionally used to model count data (i.e., Poisson or negative binomial) (Lambert 1992; Heilbron 1994). Additionally, zero-inflated count

data frequently exhibit overdispersion when modeled using a Poisson distribution because there is often more variability than allowed by the equality of mean and variance implicit to this model (Yau et al. 2003). Sources of zero inflation in ecological data include counts of a species that does not saturate all suitable habitat (Welsh et al. 2000; Cunningham and Lindenmayer 2005), counts of organisms for which certain covariate conditions make much of the available habitat unsuitable (Kuhnert et al. 2005) and studies with experimental design or data collection errors (Tyre et al. 2003). Count data from studies of the stopover-use patterns of shorebirds migrating through the interior of North America often include a high proportion of zero observations from sources analogous with these examples. Failure to account for zero inflation and overdispersion when modeling these data results in biased parameter estimates and measures of uncertainty and can lead to incorrect inference (Lambert 1992; Zuur et al. 2010). However, zero-inflation modeling methods have been developed that are capable of addressing these problems and hence improve the robustness of an analysis of zero-inflated count data (Martin et al. 2005; Zurr et al. 2010).

Because zero inflation is common in the count data of studies examining the habitat-use patterns of shorebirds migrating within the continental interior, analyses of these data are often limited to determining how wetland characteristics influence shorebird occurrence patterns. Thus, information on how wetland attributes influence the abundance distribution patterns of shorebirds among stopovers is limited. We therefore undertook the objective of applying an analysis that was capable of validly modeling this type of abundance data to optimize our interpretation and ecological insights. In addition, limited information exists on the extent to which the context of wetland habitat affects stopover use by migrant shorebirds and if patch context variables differentially influence the abundance of shorebirds when compared to intra patch variables. Hence, we separately examined and compared the relative importance of intra patch variables (i.e., variables measured within a focal wetland habitat patch) and patch context

variables (i.e., variables measured in the land area surrounding a focal wetland habitat patch) in explaining the differential use of wetland stopover habitats using multi-model inference in an information theoretic framework. Our approach involved surveys of potential wetland stopover habitat patches for shorebirds during spring and fall migration periods among several broad-scale landscapes in north central Oklahoma, US.

METHODS

Study region

The 24,372 km^2 study region is located within the Southern Great Plains of the United States and covers ten counties in north-central Oklahoma (Fig. 3.1). The region is characterized by flat topography and dominated by large areas of intensively managed cropland and rangeland with broadly dispersed suburban and urban development, remnant patches of mixed grass prairie and small forest stands (Oklahoma Department of Wildlife Conservation 2006, Albanese 2011a). A mixture of palustrine, riverine and created wetlands that contain hydroperiods ranging from ephemeral to ostensibly permanent occur in the region. Created wetlands include large reservoirs and smaller wetlands constructed for waste treatment and water storage for irrigation and livestock watering. The region is subject to extreme dry and wet periods (Woodhouse and Overpeck 1998), and extended drought conditions can severely limit wetland habitat within landscapes whereas severe weather events can rapidly inundate relatively small and discrete areas leaving abundant floodwater on the landscape.

Experimental design

Although some shorebird species breed within the region and some shorebird migrants may use uplands and wetlands as stopover habitat, we restricted our research to those species that migrate through the region and that primarily rely on and were observed foraging within wetland habitat during migration. We defined wetland shorebird habitat as areas of saturated substrate

and shallow water (water depth <16 cm) within wetlands and around wetland edges. Non-habitats were considered areas that did not meet these criteria (i.e., dry upland areas).

We randomly established ten10-km radius circular landscapes within the study region (Fig 3.1). Landscapes of this size were used because > 90% of the known foraging flight distances of shorebirds during stopover in the region were < 10 km (Farmer and Parent 1997). We quantified the area of potential shorebird habitat within each landscape using two methods. Initially, we used Environmental Systems Research Institute's ArcGIS 9.0 (1999-2004) GIS software to assemble 1.0 m resolution 1:12,000 digital ortho-image quarter quadrangles (DOQQs) from 2000, 2003-2006, and 2008. Although data varied among landscapes, below average precipitation and less wetland habitat characterized the 2004, 2005 and 2006 images, while above average precipitation and abundant wetland habitat characterized 2000, 2003, and 2008 images (Oklahoma Climatological Survey 2011). Within each landscape, we visually examined the entire extent of each DOQQ within the annual series at a 1:10,000 scale. When a discrete patch of potential habitat was identified, we delineated the broadest contiguous extent of habitat among the annual series of DOQQs as a polygon. The area within these polygons formed potential habitat patches within landscapes (Fig. 3.1). Because of logistical constraints, we did not delineate discrete potential habitat patches <1,000 m^2 or areas within channeled waterways <30 m wide. In addition, field surveys of all landscapes and habitat patches used in the final analysis were conducted with $1m^2$ color ortho images to evaluate and revise habitat delineations. Maps were marked with UTM grid lines and were used in conjunction with GPS receivers. All additional habitat patches identified during surveys and any patch boundary refinements were continuously updated in the GIS.

Bird surveys and habitat measurements

Shorebird surveys were conducted from March thru May in 2007, 2008 and 2009 and from July 15 thru October in 2007 and 2008. We used variance and effect size estimates from a

pilot study and an *a priori* regression power analysis (Lenth 2006) for sample size ($\alpha = 0.05$, $1-\beta = 0.95$) to estimate that 13% of the area of potential shorebird habitat per landscape was required to detect an effect in shorebird abundance. Additionally, previous research has suggested a maximum average residency period of 10.5 days for midcontinental shorebirds during a stopover event (Skagen and Knopf 1994; Farmer and Durbian 2006; Skagen et al. 2008). Therefore, we divided each spring and fall migration period into four 23-day survey intervals to ensure independence among our survey data and surveyed 13% to 15% of the total area of potential habitat within each landscape for shorebirds once during each survey interval.

We designed a software program to acquire a unique sample of potential habitat patches within each landscape for each survey interval. The program randomly selected 15% of the total potential shorebird habitat within each landscape for each survey. Each square meter of shorebird habitat had equal probability of selection and no area was selected more than once for a survey interval. When a square meter of habitat in a discrete patch with a total area < 5 ha was selected, the entire patch was included in the sample and surveyed during the interval. When a square meter of habitat was selected within a habitat patch > 5 ha, the 5 ha closest to the meter was delineated by the program, included in the sample and this portion of the patch was surveyed. The program randomly assigned a habitat patch for the start of surveys, arranged the remaining habitat patches along a minimum distance survey route with a road map, and provided an alternate for each habitat patch in case logistical constraints prevented a survey. In addition, it produced $1m^2$ color ortho images with UTM grid lines and the boundaries of each selected patch and these were used in conjunction with GPS receivers to conduct surveys.

Shorebird surveys were conducted during daylight hours from a vehicle or on foot, depending on the visibility or location of the habitat patch. After arriving at a habitat patch, we waited several minutes before initiating a survey. First, we recorded the presence or absence of shorebird habitat within the patch. Habitat was considered absent if habitat patches were

completely dry or if they were completely inundated with water > 16 cm in depth. If habitat was present, the patch was surveyed for shorebirds. Each habitat patch ≤ 1 ha was surveyed for five minutes during a visit and equal time was added for each additional hectare of habitat. Shorebirds were observed with a 10 x 60 spotting scope or 8 x 40 binoculars. All shorebirds observed in a habitat patch were identified and counted.

Habitat measurements were also collected during each survey of a habitat patch. Measurements were grouped into two types: intra patch and patch context. Intra patch measurements were collected within a focal patch and patch context measurements were collected from the area surrounding the focal patch. Table 3.1 provides a description of the habitat variables collected during each survey. For variables that included cover estimates, a traditional cover-class scheme was used which included the following cover classes: 0%, 1-5%, 6-25%, 26-50%, 51-75%, 76-95%, and >95% (e.g., Domin 1928; Braun-Blanquet 1964, Daubenmire 1968). Cover-class midpoints were used in the analysis. The patch context variable habitat density was estimated *post hoc* using field data and the GIS of potential shorebird habitat within landscapes. We used a kernel-density software program to estimate the density of shorebird habitat within 2 km of each habitat patch during each survey interval (Worton 1989). Field data was used to estimate the probability of the presence of different habitat types within each landscape during each interval. We incorporated these probability estimates into the kernel density function to estimate the density of shorebird habitat surrounding each habitat patch within a landscape during a survey interval. Habitat density at a 2 km spatial scale was used in this analysis because in a related study this scale best described the observed occurrence patterns of shorebirds among landscapes. A full description of the habitat density metric and the spatial scaling analysis is provided in Albanese (2011b).

Statistical analysis

An exploratory analysis of the data set revealed a large proportion of zero values for the response variable shorebird abundance (84.2 %) and evidence of overdispersion ($\emptyset$ = >2). To determine a modeling approach that would most effectively account for these issues, we initially modeled these data using several alternative modeling procedures used for count data (i.e., Poisson, negative binominal and zero-inflated models) and compared models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002). Additionally, we examined the parameter estimates of each of these models to determine if the estimates were ecologically realistic (Joseph et al. 2009) and used likelihood ratio tests to determine which zero-inflated models adequately addressed overdispersion.

Based on the results of the initial analysis (Table 3.2), we used zero-inflated negative binomial models (ZINB) (Zurr et al. 2010) to relate the abundance of shorebird species within habitat patches to intra patch and patch context variables. Using this approach, the abundance of shorebirds within a habitat patch was modeled as a product of both migratory shorebird occurrence and abundance. In ZINB, a zero-inflated logistic regression portion modeled the probability that shorebirds were absent from a habitat patch and a negative binomial regression portion modeled the number of shorebirds within habitat patches and the absence of shorebirds under certain covariate conditions. Zero values were therefore modeled using both binomial and count processes. The same pool of explanatory variables can be included in both portions of the ZINB for contribution to a final model but after model selection, each portion may contain unique combinations of variables and different parameter estimates for the same variable.

Models containing intra patch and patch context variables were modeled separately using ZINB with maximum-likelihood estimation. We used an information theoretic approach with multi-model inference to identify which models best explained observed patterns in the abundance of migratory shorebirds and to determine the relative importance and effect size of the explanatory variables within the intra patch and patch context models (Burnham and Anderson

2002). Prior to analysis, correlations among intra habitat patch and among patch context explanatory variables were examined and no variables were strongly intercorrelated ($r < 0.4$). The explanatory variables HAREA, VEG, WATMUD and SLOPE were included in both portions of the global intra patch model and the explanatory variables HDENS, LANCON, CROP and GRAZE were included in both portions of the global patch context model (See Table 3.1 for description of codes). Among the patch context variables, the variables LANCON and CROP were coded as nominal variables for the analysis. For the multi-level LANCON variable, land cover types were contrasted against the wetland land cover type (mean 36.1). For the final analysis, the alternative models in each candidate set included all possible additive combinations of the variables in each portion of the global model and a null model set (R = 625). Initially, we included year and season variables in each candidate set but because these variables did not contribute to these models, we excluded them from the final analysis.

We used AIC to compare the relative ability of alternative models to explain observed patterns. We calculated the ΔAIC and the AIC weight of each model in the set to evaluate models and to select the most parsimonious models among the candidate set. We considered all models with a ΔAIC < 6 to have support, but only selected models when the AIC value for a model was less than the AIC values of all the simpler models within which they were nested (Richards 2008). We validated the top model selected in each candidate model set by plotting Pearson residuals against fitted values and against each explanatory variable and ensuring the lack of any pattern. To determine the direction and magnitude of effects sizes for explanatory variables, we calculated mean standardized parameter estimates. We used the AIC weights to calculate composite model parameter estimates, summed Akaike weights for each parameter, unconditional standard errors and 95% confidence intervals (CI) for each parameter estimate (Burnham and Anderson 2002). All analyses were conducted using R 2.12.1 (R Development Core Team, 2010) and SAS 9.1 (Statistical Analysis System, 2003) software.

RESULTS

During the five migration periods of this study, we surveyed 14,444 potential shorebird habitat patches and observed 38,288 migratory shorebirds that included 29 species (Table 3.3). We observed 22,571 shorebirds during the three spring migration periods and 15,717 shorebirds during the two fall migration periods. During the study, shorebird habitat was present in 8,337 habitat patches at the time of a survey and shorebirds were present in 15.8% of these habitat patches.

Intra patch characteristics

The most parsimonious model to explain the abundance of migratory shorebirds using variables measured within habitat patches contained the explanatory variables HAREA, VEG and SLOPE in the logistic regression portion and HAREA, VEG, WATMUD and SLOPE in the count portion of the model (Table 3.4). This model was 2.2 times more plausible than the next top model in the set. In the logistic regression portion of the model, the summed Akaike weights of the variables WATMUD and VEG were relatively low and the 95% CI of the composite parameter estimates for these variables included zero (Fig. 3.2). This indicates that these variables were not well-supported predictors of migratory shorebird absence. Conversely, the variables HAREA and SLOPE were important predictors of shorebird absence and exhibited strong effects on the occurrence of migratory shorebirds. The highest probability of the absence of a migratory shorebird from a habitat patch was obtained when values of HAREA were small and values of the variable SLOPE were steepest (Fig. 3.3).

All four intra patch variables we measured were included in the count portion of the models in the "best model" set (Table 3.4). However, only the variables HAREA, VEG and SLOPE were well supported as important predictors of migratory shorebird abundance (Fig. 3.2). The abundance of migratory shorebirds within a habitat patch was positively related to increases in HAREA and negatively related to increases in VEG and SLOPE.

Patch context characteristics

The most parsimonious model to explain the abundance of migratory shorebirds within a habitat patch using patch context variables only included the explanatory variable HDENS in the logistic regression portion of the model (Table 3.4). The probability of the absence of migratory shorebirds from a habitat patch was greatest when HDENS was low (Fig. 3.3). The variables HDENS, LANCO and GRAZE were well-supported predictors of migratory shorebird abundance (Fig. 3.4). The results indicate that shorebird abundance was positively related to increases in the variables HDENS and GRAZE. For the nominal variable LANCON, the forest/shrubland, grassland and developed land cover types were negatively related to shorebird abundance when compared to the wetland land cover type (Fig. 3.5).

The AIC value of the top model selected from the candidate model set that included patch context variables was lower than the top model selected from the candidate model set that included intra patch variables (Table 3.4). These results suggest that given the data and candidate model sets, the top model containing patch context variables was a better approximating model of shorebird abundance than the top model containing intra patch variables.

DISCUSSION

Intra patch characteristics

Our analysis of en route wetland habitat use by migratory shorebirds within the south central Great Plains revealed that shorebirds stopover in greater abundance in large wetland habitats that are sparsely vegetated and dominated by shallow slope angles. Additionally, small habitat areas and habitats dominated by steep slope angles were identified as sources of zero-inflation among intra patch variables. Previous works by others have also reported a positive association between shorebird habitat area and migratory shorebird occurrence and abundance within wetlands (Taft et al. 2002; Skagen et al. 2005; Webb et al. 2010). However, we are

unaware of any studies that have examined the influence of slope on wetland stopover use by migratory shorebirds. A possible explanation for the negative association of migratory shorebirds with slope may be that wetland habitats dominated by steep slope angles were often characterized by an invariant water depth profile and shorebird habitat limited to wetland edges. Greater topographic variation within a wetland broadens the diversity of foraging depths available to shorebirds and increases shorebird diversity and abundance within wetlands (Colwell and Taft 2000; Taft et al. 2002). Furthermore, steep-sided wetland habitats may limit the ability of shorebirds to detect potential predators because views of the surrounding landscape are obscured. Feeding is the primary behavior exhibited by shorebirds during a stopover in the wetlands of the central Great Plains (Davis and Smith 1998a; DeLeon and Smith 1999). Habitats with visual obstruction increase shorebird behaviors associated with vigilance during foraging (Metcalfe 1984). Shorebirds may not use steep-sided wetlands because increased vigilance may come at the expense of time spent feeding.

Our results are consistent with other studies that have reported a negative relationship between increased vegetation structure within a wetland and wetland stopover use by migrating shorebirds (Weber and Haig 1996; Davis and Smith 1998b, Niemuth et al. 2006). Though, it is noteworthy that our results indicate increased vegetation structure was not a source of zero inflation in our count data. Contrastingly, Farmer and Durbain (2006) found that vegetation attributes of wetlands in northwestern Missouri, US were the most important factors to affect the probability of shorebird detection in a wetland stopover. However, their study only included wetlands within a National Wildlife refuge complex and these wetlands may have been more consistently characterized by greater vegetation structure than the broader range of wetland habitats included in our study. Furthermore, the survey methods used differed between the studies. We therefore suggest further examination on how vegetation may differentially influence

the detection of shorebirds within wetlands in other parts of the midcontinental interior of North America.

Our results suggest that the amount of shallow water and saturated substrate within shorebird habitat was a poor predictor of shorebird abundance. While other studies have demonstrated the potential importance of mud flat and shallow water availability to stopover use by migrating shorebirds (Davis and Smith 1998b), we suggest that we failed to find a relationship because we included many different shorebird species in our analysis. Because shorebirds have different niches along a water depth continuum (Davis and Smith 2001), a community-level analysis may be inadequate for explaining how patterns in water depth and mud exposure influence the occurrence and abundance distribution of shorebirds within wetland stopovers because these variables are more relevant at a species level.

Patch context characteristics

We found that wetland stopovers in low habitat density conditions were the source of zero inflation among the patch context variables we measured and habitat density was an important predictor of the abundance of shorebirds within wetland stopovers. Other studies examining the stopover-use patterns of shorebirds migrating through the central Great Plains have also reported a positive relationship between wetland area in the surrounding landscape and shorebird distribution patterns within wetlands (Skagen et al. 2005; Niemuth et al. 2006; Webb et al. 2010). Additionally, these results are consistent with the findings of a related study in which shorebirds occurred in 6% of surveyed habitat patches when habitat density was low (density < 0.06/2 km r^2), but occurrence reached 56% when habitat density was high (density > 0.16/2 km r^2) (Albanese 2011b). Furthermore, we found a positive relationship between shorebird abundance and the area of wetland shorebird habitat within landscapes (Albanese 2011a). Collectively these findings further support the idea that initial stopover selection by migrant birds is made using broad scale assessments of potential habitat and this initial choice of landing site

may ultimately determine fine scale habitat-use patterns (Jenni and Schaub 2003; Buler et al. 2006). Thus, shorebird habitat patches in low-density conditions may not be used because high-density habitat at broad spatial scales is the basis for initial stopover selection.

Grazing intensity in the area surrounding a wetland habitat patch was also an important predictor of shorebird abundance. We offer several explanations for this positive association. First, within the south central Great Plains, grazing was found to increase the biomass of some invertebrate taxa within wetlands and grazed wetlands had enhanced invertebrate diversity when compared to unmanaged wetlands and wetlands managed with other common methods (Davis and Bidwell 2008). The abundance and distribution of aquatic invertebrates influences the use of wetlands by migrating shorebirds (Davis and Smith 1998b; Andrei et al. 2008). The abundant and diverse invertebrate prey resources associated with grazing may positively affect the use of these wetland habitats by migrant shorebirds. Secondly, grazing decreases plant biomass and can create a mosaic of open and vegetated patches within and around wetlands that may be attractive to shorebirds. Sparse vegetation cover and wetlands with an interspersion of open and vegetated areas have been associated with an increase in wetland stopover use by migratory shorebirds (Davis and Smith 1998b; Webb et al. 2010). Our data also supports this explanation, as grazing intensity was negatively correlated with the intra patch variable VEG, which in turn was negatively associated with shorebird abundance. Lastly, shorebirds were often observed foraging among livestock within wetlands and around wetland edges during this study. We hypothesize that the movements of livestock may increase the exposure of aquatic invertebrate prey to foraging shorebirds. Livestock foot traffic may suspend benthic invertebrates for gleaning shorebirds and increase the pliability of soils for shorebird species pecking and probing these substrates. We recommend further investigation into the relationship between wetland stopover use by migratory shorebirds and grazing within the southern Great Plains, but stipulate the

consideration of the potential negative impacts of grazing on water quality and the entire wetland community (Fleischner 1994; Freilich et al. 2003; Asner et al. 2004).

When compared to shorebird habitat in a wetland context several land cover types were negatively associated with shorebird abundance. Developed and forest/shrubland cover exhibited the strongest negative effects to migratory shorebird abundance. We also found a negative relationship between the abundance of shorebirds and habitat patches in a grassland dominated context. We suggest that the negative influence of these land cover types on the abundance of migratory shorebirds may be attributed to a preference among many shorebird species for open habitats with minimal visual obstruction. Foraging shorebirds are often associated with open habitats and open habitats may enhance predator detection (Metcalfe 1984; DeLeon and Smith 1999; Colwell 2010). The land cover contexts negatively associated with shorebird abundance were frequently characterized by less open conditions. Developed lands often contained relatively tall man-made structures, forest and shrubland contained tall woody vegetation (>2.5 m), and grassland, in the absence of disturbance, contained above ground vegetation cover throughout the year that was often characterize by tall glades of grass. Conversely, the influence of pasture, barren and cropland land cover types on migratory shorebird abundance was negligible. Pastures often experienced intense livestock grazing and frequent vegetation removal for livestock forage. The dominant crop within the study area was winter wheat (*Triticum sp.).* This crop is immature and low in stature during much of the spring migration period and harvested in summer, and these croplands are tilled in late summer during the fall migration period. Barrens predominantly lacked vegetation cover. Consequently, all of these land cover contexts generally encompassed shorebird habitat patches in relatively open conditions comparable to those present in a wetland context.

Still, results from other studies examining the response of migrant shorebirds within the mid-continental interior of North America to the land cover context of wetlands have been

equivocal. For example, Skagen et al. (2005) found that the area of cropland surrounding focal wetlands positively affected stopover use by some migrant shorebird species, but they found no relationship between shorebird occurrence and grassland area. In contrast, Webb et al. (2010) reported no relationship with the area of cropland or grassland surrounding focal wetlands and shorebird abundance. However, both studies measured the area of these land cover types within buffers ranging from 1 to 10 km, and the amount of land cover within these buffers may not have reflected the dominant land cover type immediately adjacent to the focal wetlands. The influence of land context may be scale dependent as organisms function within a range of scales during and among different life history stages (Addicott et al. 1987; Wiens 1989). Although evidence suggests that migrant shorebirds may initially respond to wetland habitat at broad spatial scales (Albanese 2011a, 2011b), these results suggest that shorebirds may respond to the land context of a wetland stopover at finer scales that are more proximal to the focal patch than previously considered. Thus, to fully understand these patterns we recommend that future research consider the full range of scales at which land cover context may influence wetland stopover selection and use by migratory shorebirds.

Conclusions

In order to conserve the wetland stopovers essential for shorebirds to successfully complete migration through the central Great Plains of North America, it is first necessary to have a clear understanding of the basic habitat requirements of these species during this period. Our study is the first that we are aware of to identify patch context variables, when compared to within wetland habitat characteristics, as important if not superior predictors of migratory shorebird abundance within wetland stopovers. Our results highlight the need for further investigations into the potential role of landscape context variables in explaining en route shorebird occurrence and abundance patterns. Furthermore, we encourage the use of zero-inflated modeling to explicate the abundance patterns of these migrants from count data

containing many zero values. With this modeling approach, we were able to explain the en route abundance distribution patterns of migrant shorebirds and make strong inference on the importance of different wetland stopover characteristics. Additionally, we identified several sources of zero inflation that when considered, may enable more efficient census and research techniques and better facilitate conservation efforts for these species. For example, theory suggests that broad-scale characteristics are used as initial stopover selection cues and small and discrete wetland habitats may be below the spatial threshold used for initial selection (Hutto 1985; Moore and Aborn 2000; Deppe and Rotenberry 2008). These habitats are geographically isolated from wetland complexes capable of providing high-density shorebird habitat and therefore, may remain consistently unused even if all other habitat attributes are suitable for stopover use by shorebirds. Thus, these wetland habitats may be of limited value to shorebird conservation and monitoring programs with restricted resources.

Conservation management of the migratory shorebirds in the region should aim to provide wetland stopovers with large expanses of saturated and shallow water habitat that is sparsely vegetated and shallow sided. These stopovers should be in areas with the potential to provide high-density habitat at a 2 km scale and encompassed in an open land cover context. In addition, our results suggest grazing as a potential management technique for wetland stopovers, but we strongly suggest additional investigation before implementation. Because our analysis included a wide range of the shorebird species that migrate through the region, these management recommendations should be generally applicable and benefit a diverse shorebird assemblage. We recommend comparable research be conducted in other portions of the Great Plains to aid in the refinement of these management recommendations.

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Table 3.1. Description of the intra patch and patch context variables measured at shorebird habitat units that were surveyed in north-central Oklahoma, US, 2007-2009.

Variable	Code	Description
Intra patch		
Shorebird habitat area	HAREA	The cover estimate of saturated substrate and shallow water (< 16 cm) present multiplied by the total potential habitat within the focal patch.
Shallow water and saturated substrate cover	WATMUD	The proportion of the habitat area within a focal patch covered by shallow water (< 16 cm) and thus the inverse of saturated substrate cover.
Vegetation cover and dominate height	VEG	The multiplicative interaction between the cover estimate of emergent vegetation within the portion of a focal patch covered by shorebird habitat and the dominant height category of the emergent vegetation cover. The height categories were: (0) 0 m, (1) < 0.5 m, (2) > 0.5 m to < 1.5 m, and (3) > 1.5 m.
Dominate slope	SLOPE	The range of the dominant slope angle between the interface of the portions of a focal patch covered by shorebird habitat and non-habitat. The slope categories were: (1) < 20°, (2) >20° to < 45°, and (3) > 45°.
Patch context		
Habitat density [a]	HDENS	The density of shorebird habitat at a 2 km spatial scale measured at the centroid of a focal patch. Habitat density estimates ranged from 0 to 1 where 1 equaled complete cover of shorebird habitat.
Dominant land cover	LANCO	The dominant land cover type abutting the focal patch. The land cover types were wetland, barren, forest/shrubland, grassland, pasture, cropland and developed.
Crop cultivation	CROP	The presence or absence of active annual crop cultivation abutting the focal patch.
Grazing intensity	GRAZE	The grazing intensity on the area abutting a focal patch. The categories were: (0) no indication of grazing, (1) low intensity grazing: tussock structures present among vegetation indicating some selective grazing, some closely grazed patches but none > 1m, and signs of light livestock foot traffic and (2) high intensity grazing: vegetation within habitat cropped, indicating non-selective grazing by livestock, and signs of heavy livestock foot traffic.

[a] The habitat density estimates for each patch were calculated using the methods described in Albanese (2011b).

Table 3.2. The degrees of freedom (DF), ΔAIC, Akaike weights (w_i) and likelihood ratio test statistics (p) of global regression models of shorebird count data dependent on intra habitat patch or habitat patch context variables. The AIC values were compared among standard and zero inflated Poisson and negative binomial models to access the fit of the shorebird count data to the underlying model. Likelihood ratio tests were used to test if the variance structures of the zero inflated Poisson and negative binomial models were equal.

Model Type	DF	ΔAIC	w_i	P
Global intra patch models				
Zero inflated negative binomial	11	0	1	< 0.0001
Standard negative binomial	6	575	<0.0001	
Zero inflated Poisson	10	62643	<0.0001	
Standard Poisson	5	130351	<0.0001	
Global patch context models				
Zero inflated negative binomial	21	0	1	< 0.0001
Standard negative binomial	11	851	<0.0001	
Zero inflated Poisson	20	64303	<0.0001	
Standard Poisson	10	121563	<0.0001	

Table 3.3. List of the total number of migratory shorebird species encountered within shorebird habitat during spring and fall migration periods in north-central Oklahoma, US, 2007-2009. Shorebird habitat was defined as shallow water (< 16 cm) and saturated substrate within and surrounding wetlands.

Species	Spring	Fall
Black-bellied Plover *(Pluvialis squatarola)*	96	213
American Golden-Plover *(Pluvialis dominica)*	10	1285
Semipalmated Plover *(Charadrius semipalmatus)*	28	39
American Avocet *(Recurvirostra americana)*	477	1072
Black-necked Stilt *(Himantopus mexicanus)*	37	20
Willet *(Tringa semipalmata)*	16	6
Lesser Yellowlegs *(Tringa flavipes)*	359	750
Greater Yellowlegs *(Tringa melanoleuca)*	266	307
Solitary Sandpiper *(Tringa solitaria)*	20	39
Whimbrel *(Numenius phaeopus)*	22	0
Long-billed Curlew *(Numenius americanus)*	16	0
Hudsonian Godwit *(Limosa haemastica)*	64	0
Marbled Godwit *(Limosa fedoa)*	2	19
Ruddy Turnstone *(Arenaria interpres)*	82	1
Red Knot *(Calidris canutus)*	0	7
Sanderling *(Calidris alba)*	104	39
Dunlin *(Calidris alpina)*	227	0
Semipalmated Sandpiper *(Calidris pusilla)*	3364	392
Western Sandpiper *(Calidris mauri)*	713	1071
Least Sandpiper *(Calidris minutilla)*	1638	6620
White-rumped Sandpiper *(Calidris fuscicollis)*	4602	0
Pectoral Sandpiper *(Calidris melanotos)*	319	409
Baird's Sandpiper *(Calidris bairdii)*	2996	1082
Unidentified peep[a]	577	89
Buff-breasted Sandpiper *(Tryngites subruficollis)*	4	3
Long-billed Dowitcher *(Limnodromus scolopaceus)*	1617	1260
Wilson Snipe *(Gallinago delicate)*	207	298
Stilt Sandpiper *(Calidris himantopus)*	1125	354
Wilson's Phalarope *(Phalaropus tricolor)*	3577	322
Red-necked Phalarope *(Phalaropus lobatus)*	6	20

[a] Identification of individual was determined to be one of the follow species: *Calidris pusilla, C. mauri, C. minutilla, C. fuscicollis, C. bairdii*

Table 3.4. Zero-inflated negative binomial regression model-selection results for shorebird count data dependent on inter patch or patch context variables. The explanatory variables included in each portion of the selected models are given and the abbreviation codes used for these variables are provided in Table 3.2. The AIC value of the top model of each candidate set, and the ΔAIC and Akaike weights (w_i) of all the top models selected (ΔAIC < 6 [a]) are provided.

Zero-inflated logistic portion	Negative binomial count portion	AIC	ΔAIC	w_i
Intra patch candidate models				
HAREA + VEG + SLOPE	HAREA + WATMUD + VEG + SLOPE	15980	0	0.31
HAREA + WATMUD + VEG + SLOPE	HAREA + VEG + SLOPE		1.58	0.14
HAREA + SLOPE	HAREA + WATMUD + VEG + SLOPE		2.27	0.10
HAREA + SLOPE	HAREA + VEG + SLOPE		5.71	0.02
Patch context candidate models				
HDENS	HDENS + LANCO + GRAZE	15125	0	0.39

[a] Alternative candidate models were only selected for the "best model" sets when the AIC value for a model was less than the AIC values of all the simpler models within which they were nested (Richards 2008).

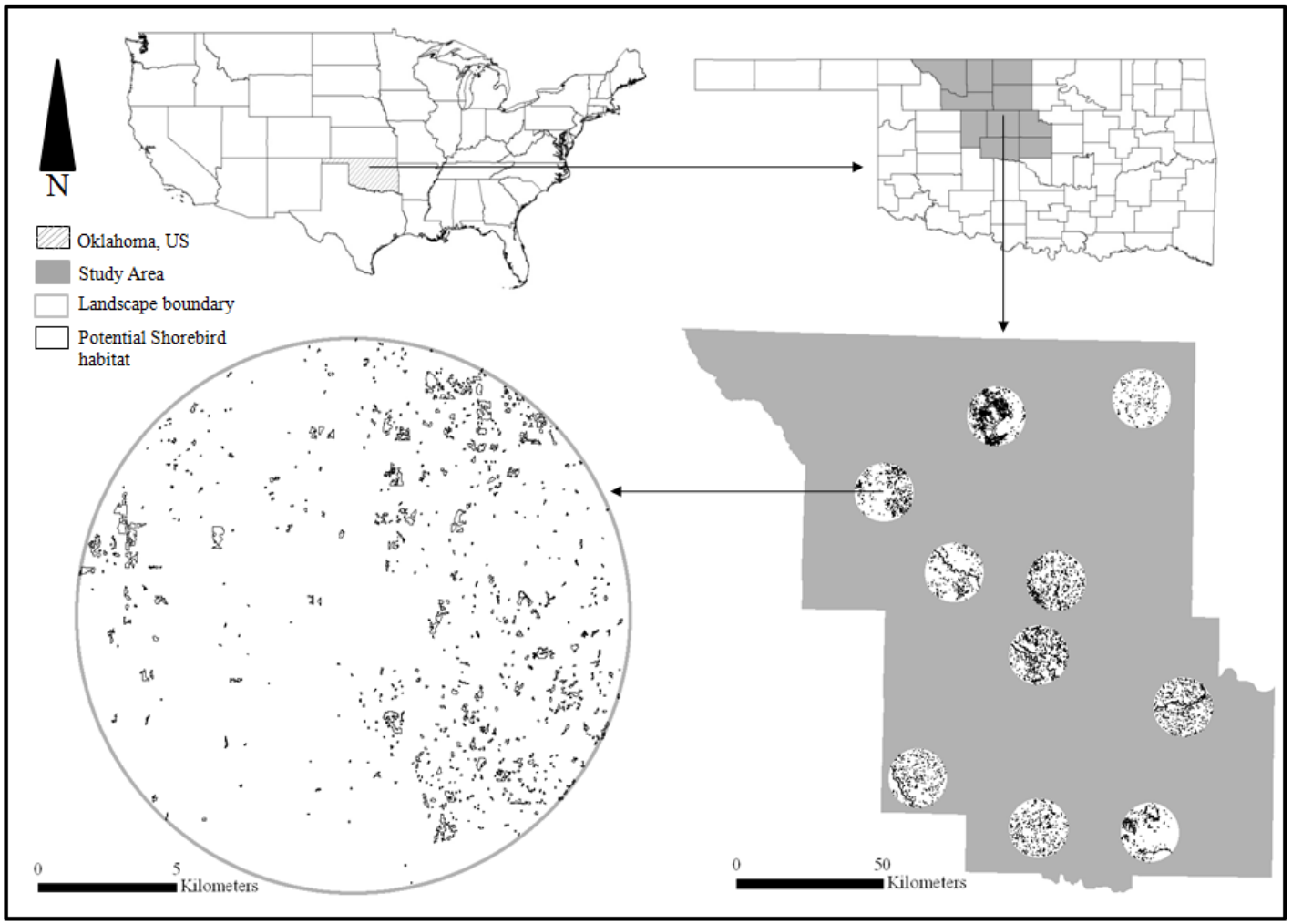

Figure. 3.1. Study area and landscapes in north-central Oklahoma, US. The locations of study landscapes within the study area are given with an enlarged landscape illustrating the extent and distribution of the potential shorebird habitat patches surveyed.

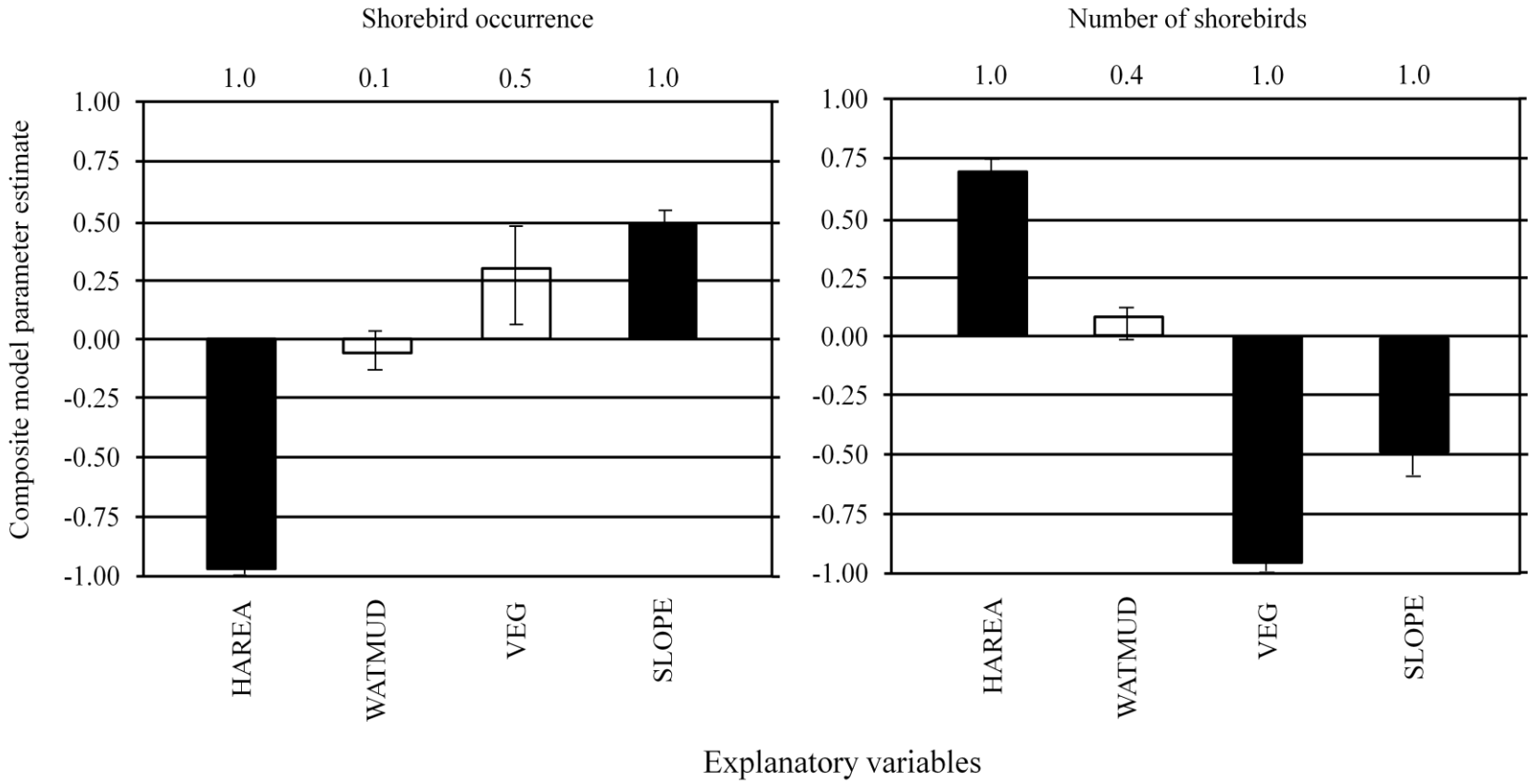

Figure. 3.2. Relative effect size of intra patch explanatory variables (standardized model-averaged coefficients, mean ± SE) on the absence (left side) and abundance (right side) of migratory shorebirds within shorebird habitat patches. The relative importance of each explanatory variable is given above each bar. Black bars indicate parameter estimates with 95% confidence intervals that did not include zero. The abbreviation codes and description of each explanatory variable are given in Table 3.2.

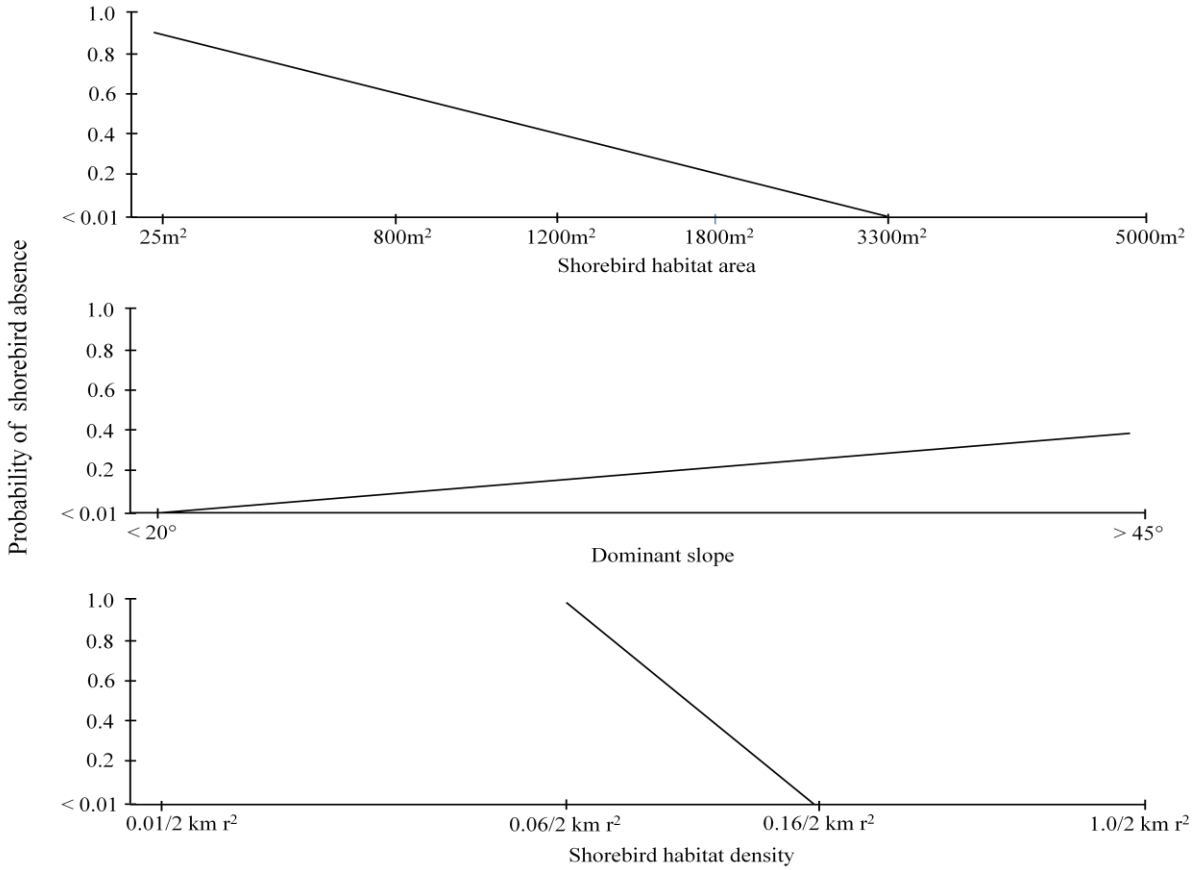

Figure. 3.3. Fitted curves from the logistic regression portion of the zero-inflated negative binomial models. The vertical axis show the probability of the absence of shorebirds from a habitat patch in relation to the explanatory variables listed on each horizontal axis. Among all of the explanatory variables included within the logistic regression portion of the models, the 95% confidence intervals of the parameter estimates for each of these explanatory variables did not include zero.

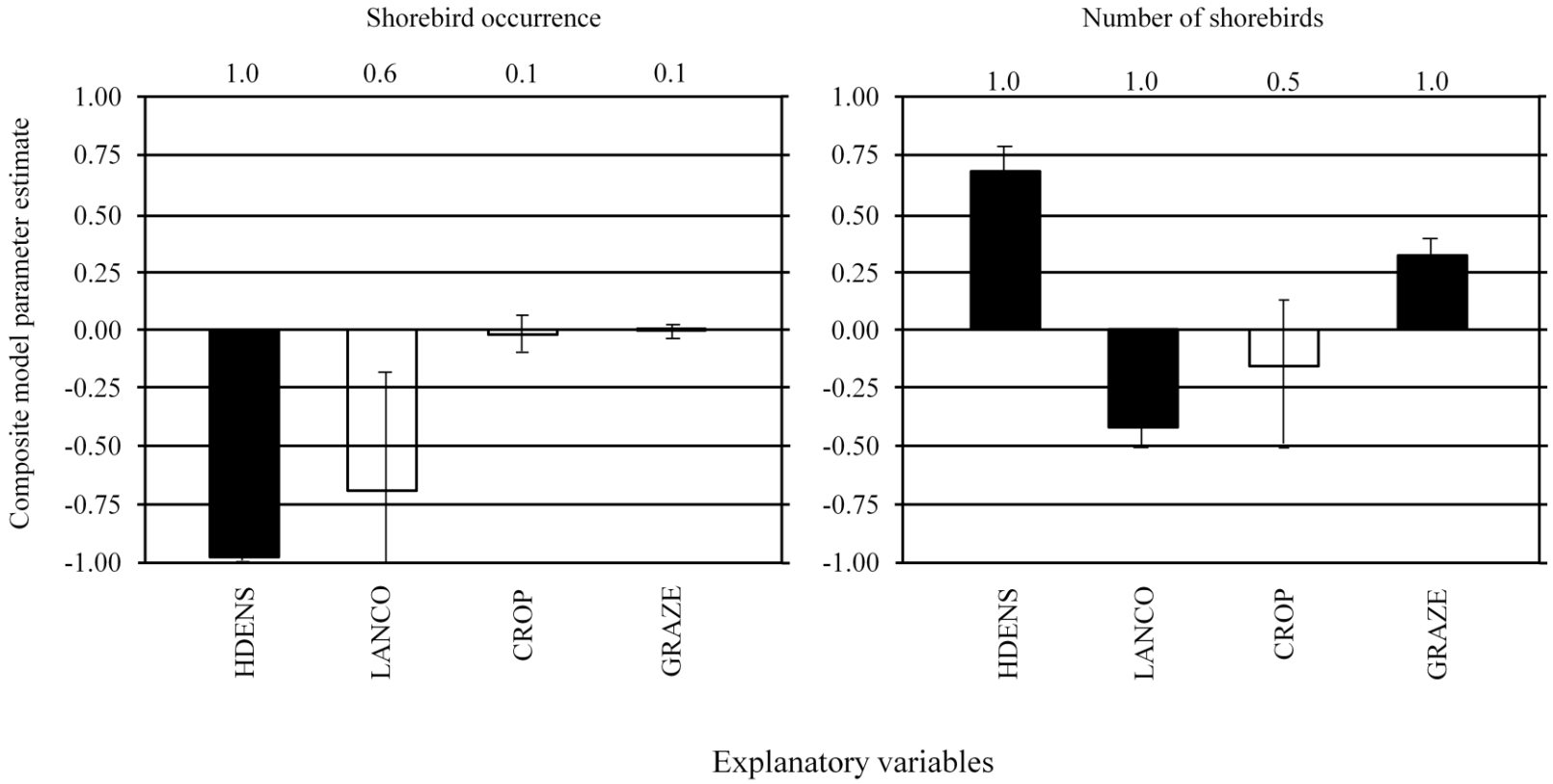

Figure. 3.4. Relative effect size of patch context explanatory variables (standardized model-averaged coefficients, mean ± SE) on the absence (left side) and abundance (right side) of migratory shorebirds within shorebird habitat patches. The relative importance of each explanatory variable is given above each bar. Black bars indicate parameter estimates with 95% confidence intervals that did not include zero. The abbreviation codes and description of each explanatory variable are given in Table 3.2.

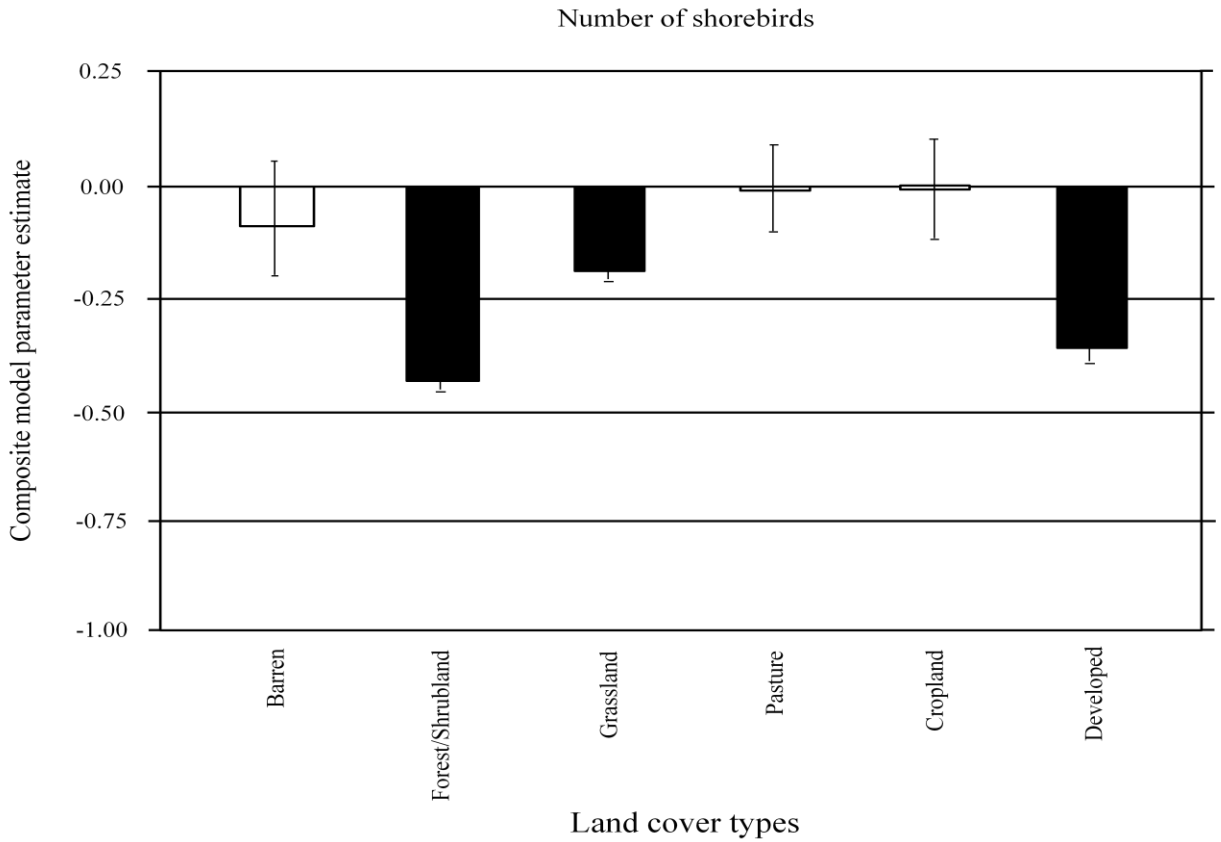

Figure. 3.5. Relative effect size of each land cover type in the dominant land cover explanatory variable (standardized model-averaged coefficients, mean ± SE) on the abundance of migratory shorebirds within shorebird habitat patches. Dominant land cover was an important predictor in the negative binomial count portion of the patch context model and was analyzed as a nominal variable with land cover types contrasted against the wetland land cover type. Black bars indicate parameter estimates with 95% confidence intervals that did not include zero.

VITA

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Candidate for the Degree of

Doctor of Philosophy

Dissertation: A MUULTI-SCALE EXAMINATION OF STOPOVER HABITAT USE BY MIGRANT SHOREBIRDS

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Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: A MULTI-SCALE EXAMINATION OF STOPOVER HABITAT USE BY MIGRANT SHOREBIRDS

Pages in Study: 120 Candidate for the Degree of Doctor of Philosophy

Major Field: Natural Resource Ecology and Management

Scope and Method of Study: Surveys of wetland stopover habitats for migrant shorebirds were conducted within broad-scale landscapes in north-central Oklahoma from 2007 thru 2009. The response of wetland shorebird habitat to weather patterns was examined and a metric was developed to measure changes in the composition and configuration of shorebird habitat within landscapes. I subsequently examined the response of shorebirds to the density of wetland habitats at different spatial scales, the amount of different wetland habitats and peripheral land cover types at a landscape level and intra habitat and habitat context characteristics at a patch level.

Findings and Conclusions: Precipitation, temperature, solar radiation and wind speed best explained the occurrence of wetland habitat, but relationships varied with time and among wetland types. Shorebird occurrence patterns within wetland stopover habitats were best explained by habitat density at a 2 km scale and stopover use increased with habitat density at this scale. The abundance and diversity of shorebirds were positively related to the area of wetland habitat within landscapes regardless of the composition of other land cover types, but relationships with wetland habitat types differed among shorebirds based on migration distance and breeding status. Within wetland stopovers, shorebird abundance increased with habitat area, habitat density and grazing intensity and was negatively related to vegetation structure, dominant slope and some land cover contexts. I conclude that broad-scale factors related to the amount and context of wetland habitat are important to explaining migrant shorebird distribution patterns during their stopover at wetlands in north-central Oklahoma.

ADVISER'S APPROVAL: Craig A. Davis